

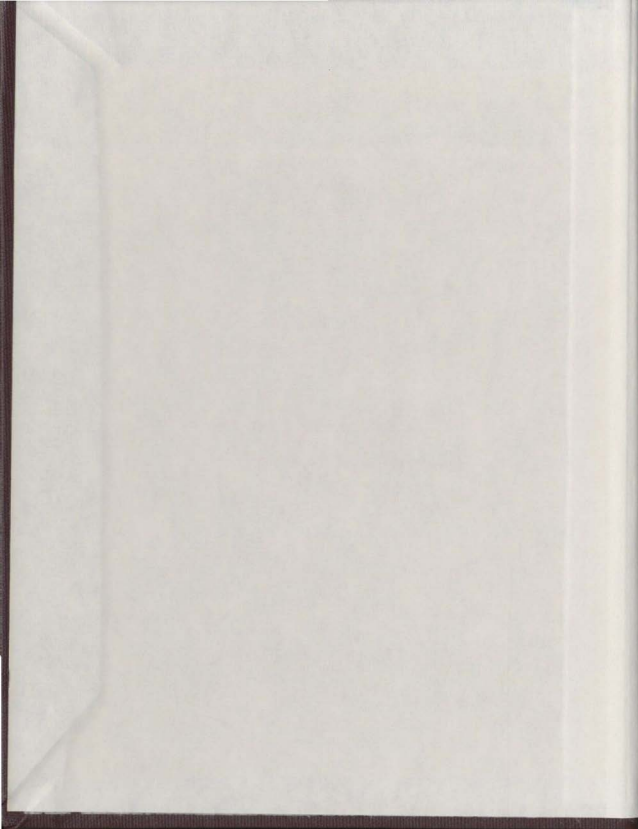
HOMING IN LEACH'S STORM PETREL
OCEANODROMA LEUCORHOA LEUCORHOA

CENTRE FOR NEWFOUNDLAND STUDIES

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Homing in Leach's Storm Petrel

Oceanodroma leucorhoa leucorhoa.

by

Ⓒ Christopher John Spencer, B.A. B.Ed.

A Thesis submitted in partial fulfillment
of the requirements for the degree of
Master of Science

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St. John's

Newfoundland

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Abstract

During the summers of 1975 and 1976 homing behaviour was studied in Leach's Storm Petrel, Oceanodroma leucorhoa leucorhoa. Five displacements involving 148 different birds were performed. Homing times and success were highly variable even amongst control home island releases. Distance and direction of displacement had no marked effect on medium range releases. However, near the breeding island, downwind birds performed better than upwind birds, presumably as a function of olfactory cues emanating from the island. Birds displaced inland did not perform as well as those released an equal distance away but at water's edge. Incubation shift length, sex, breeding experience, or previous displacement experience did not appear to affect homing times. Weight was important : heavy birds homed sooner losing weight en route while light birds took more time while gaining weight. Both physical size and motivational factors are implicated in this phenomenon.

In orientation activity chambers, adults at four release sites did not orient homewards. However some of these adults, as well as adults tested on the home island, faced downwind. In contrast, chicks were less active and randomly oriented.

A food sampling study indicated that Leach's Storm Petrel may obtain many of their prey items within the environs of the breeding colony though to procure one major group, myctophid fishes, a one way trip of at least 125 km

to the SW would be necessary. Another prey species, Hyperia galba, is specific to inshore waters. These two food types could provide positional information to a petrel.

While netting birds, record was kept of the number of birds that struck the net. The number of collisions was nonsignificantly negatively correlated with wind speed, illumination level, and the number of times the net had been at one spot. However, all but one of the interactions were significant suggesting the variables had real though weak effects.

Taken together the results were interpreted as being consistent with the homing literature in indicating a limited redundancy of orientation systems and a situation dependent hierarchy of cues. Compass usage was not demonstrated with Leach's Storm Petrel but suggestions for further work were made.

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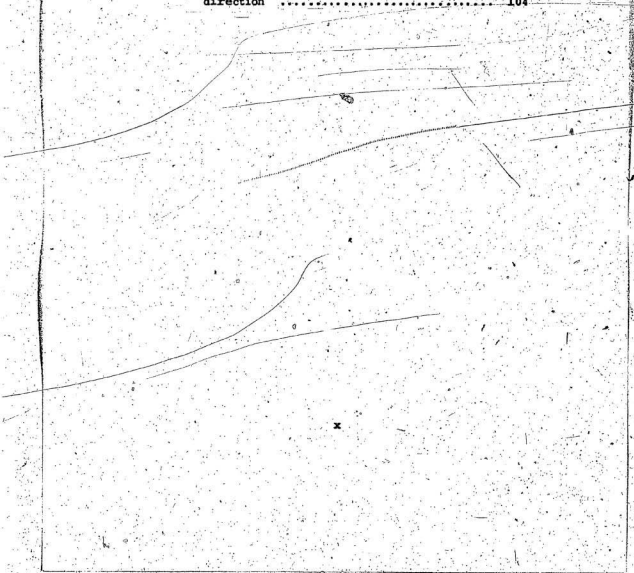
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INTRODUCTION

This thesis examines the homing ability of Leach's Storm Petrel: Oceanodroma leucorhoa leucorhoa. In particular, information employed by the birds to orient and the motivational factors conducive to good performance were studied. The literature review covers recent work in navigation and homing, aspects of petrel biology relevant to an examination of their homing abilities, and finally previous homing studies with Leach's Storm Petrel.

Homing

In the last 25 years, the phenomenon of homing in birds has received an increasing amount of attention. Since 1965 homing has been frequently reviewed (Schmidt-Koenig, 1965, 1976; Wallraff, 1967; Matthews, 1968; Griffin, 1969; Adler, 1971; Galler, Schmidt-Koenig, Jacobs and Belleville, 1972; Keeton, 1974; Emlen, 1975).

Orienting Behaviours Used by Homing Organisms

Schmidt-Koenig (1976) and others adopt the following classification of orienting behaviours first proposed by Griffin (1952). Type I or piloting is simply steering a course with reference to familiar landmarks. Madison (1972) has suggested "familiar landmarks" be changed to "direct sensory cues" so that homing based on such stimuli as smells

and sounds emanating from the goal might be incorporated in this category. In support of this amendment, Emlen (1975) added the descriptors "visual or otherwise" to landmarks.

Type II orienting describes the ability to fly in a certain direction (i.e. maintain a compass course) even when crossing unfamiliar territory. The emphasis here is on maintaining a heading, a process considered simpler and distinct from choosing a bearing (Schmidt-Koenig, 1965; Emlen, 1975).

Type III is true navigation or the ability to orient towards home without reference to known landmarks even when displaced to unfamiliar areas. Schmidt-Koenig (1965) and Emlen (1975) have subdivided Type III further into reverse displacement orientation or maintaining reference to a goal through some inertial system (implying that the necessary information is gathered during the displacement process) and bicoordinate navigation or determining reference to a goal through a grid of coordinates composed of two or more cues.

Type III has been demonstrated only in Manx Shearwaters Puffinus puffinus (Matthews 1954a, 1964) and in Pigeons, Columbia Livea (Wallraff, 1967; Keeton, 1974; and Walcott, 1974). Such a demonstration requires goal orientation under one of the following conditions. (1) The animals' entire history is known to the extent that it can

be proven they have never been near the release site (Wallraff, 1967; Keeton, 1974). (2) The animal is displaced far enough to preclude the use of direct sensory cues into habitat it would never voluntarily enter. For example pigeons were released 80 miles out to sea (Walcott, 1972b, 1974).

Even though neither of these conditions was met in other displacements, many species have homed over impressive distances -- hundreds and thousands of kilometres (Leach's Storm Petrel, Griffin, 1940; Griffin and Goldsmith, 1955; Billings, 1968; Laysan Albatrosses, Diomedea immutabilis, Kenyon and Rice, 1958; Fisher, 1971; Purple Martins, Progne subis, Southern, 1968; Bank Swallows, Riparia riparia, Downhower and Windsor, 1971; Audubon's Shearwater, Puffinus lherminieri, Hatch, 1974). Many birds home to their nesting sites of the previous year undertaking migrations of thousands of kilometres (e.g. Mallard Duck, Anus platyrhynchos, Dwyer and Derrickson, 1973; Lee and Kruse, 1973; many procellariiformes, Lack, 1954, 1966, 1968 and many others). Wintering sites are also specific (e.g. Sparrows of the genus Zonotrichia, Ralph and Mewaldt, 1976; Starlings, Sturnis vulgaris, Perdeck, 1967).

To explain Type III navigating, several models have been proposed (Schmidt-Koenig, 1965; Matthews, 1968; Keeton, 1974; Emlen, 1975). The one favoured by recent evidence is Kramer's Map and Compass model (In Keeton, 1974; Emlen, 1975),

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which suggests that an orienting organism performs two operations. In the map step, it determines both its position relative to home and the theoretical homeward direction. In the compass step, the theoretical direction is transposed into the actual direction in the field with the aid of one or more of its compass systems. Of these two components, only the existence of the compass (solar, stellar, or geomagnetic) is supported by data, the map at present remaining a vague construct (Keeton, 1974; Emlen, 1975). Whether the information forming the map is derived from known cues (to be discussed) or some other source remains to be seen.

One avenue of exploration concerns release site bias. Keeton, (1971b, 1973, 1974) reports several release sites where pigeons depart nonrandomly in consistently incorrect directions. Each site is characterized by its own effect on orientation behavior. Yet most pigeons return home in good times. From this Keeton infers that they are reading their maps correctly, but that the maps at these particular sites are distorted. The only anomaly of these sites so far uncovered is a loss in radio transmission (Keeton, 1971b). The relevance of this finding is unclear.

Cues Used to Orient

There are many cues employable by birds to direction find (Keeton, 1974; Emlen, 1975). These may be used singly in Type I or Type II orienting or combined in some manner to permit Type III navigation. Different species may use different sets of cues and within sets there are definite preferences. Thus experienced pigeons use the sun.

as a compass when it is visible or geomagnetism as a compass under overcast (Keeton, 1974). In contrast, Indigo Buntings, Passerina cyanea, a nocturnal migrant, orient by stellar cues when available and geomagnetic cues when they are not, (Emlen 1975, Emlen, Wiltschko, Demong, Wiltschko and Bergman, 1976).

In the following review, cues have been classified by sensory system.

1) Visual Cues. These have been further categorized as being topographical, solar, or stellar.

a) Topographical Cues. Because of their salience, topographic features were once assumed to underly most orienting (Emlen 1975; Matthews, 1968, 1973). With pigeons, the only evidence for use of landmarks indicates they may be important at a near range (1 - 2 km) of the goal (Schmidt-Koenig and Schlichte, 1972; Keeton, 1974; Walcott, 1974), or else they serve to detour the bird (Wagner, 1972; Emlen 1975). Otherwise landmarks are not used as aids in orienting (Graue, 1963; Schmidt-Koenig, 1965, 1972; Walcott and Mitchener, 1967, 1971; Wallraff, 1967; Keeton, 1969, 1974; Walcott, 1972 a,b 1974; Schmidt-Koenig and Schlichte, 1972; Schlichte, 1973; Alexander and Keeton, 1974).

It may be that migrants make more use of topographical cues, especially at the end of their journey (Ballrose, 1963, 1972) but, if so, their importance is secondary (Emlen, 1975).

This is emphasized by numerous radar reports of birds remaining oriented while flying either completely within or on top of clouds (e.g. Griffin, 1972, 1973; Williams, Williams, Teal and Kanwisher, 1972).

b) Solar Cues. Several ways the sun might provide positional information have been proffered (notably Matthews, 1968, 1973). Most likely the sun, when available, is used entirely as a compass, the relevant cue being its azimuth position, and this ability includes compensation for the passage of time (a "biological clock") (Schmidt-Koenig, 1965, 1972, 1976; Wallraff, 1967; Walcott and Mitchener, 1967, 1971; Keeton, 1969, 1970, 1974; Walcott, 1972 a,b 1974; Wallraff and Graue, 1973; Alexander and Keeton, 1974). The time compensated sun compass is a wide spread phenomenon occurring in many species of animals (Schmidt-Koenig, 1976).

For nocturnal migrants there is some indication that sight of the sun's position at sunset is necessary for proper orientation (Emlen, 1975).

c) Stellar Cues. Potentially, the stars could provide the basis for true navigation. Many species of songbirds have been shown to adopt an appropriate migratory orientation when placed in an orientation chamber under clear skies at night (Schmidt-Koenig, 1965; Emlen and Emlen, 1966; Matthews, 1968; Emlen, 1971, 1972, 1975; Wallraff, 1972 a; Wiltschko and Wiltschko, 1974). Emlen (1972) has clearly shown that

for the mature Indigo Bunting the relevant stimuli are the star patterns clustered in the circumpolar region. Time compensation is not a part of this ability (Emlen, 1972). It has not been demonstrated that any species employs stellar information to home as opposed to adopting a migratory orientation (Schmidt-Koenig, 1965; Matthews, 1968; Keeton, 1974; Emlen, 1975).

d) Other Visual Cues. Polarized light is detectable by pigeons (Kreithen and Keeton, 1974 b), an ability that may help them determine the sun's position in the absence of direct sight of it. However, this offers no help in explaining orientation under overcast. Furthermore, its relevance to homing has not been demonstrated (Kreithen and Keeton, 1974 b; Keeton, 1974).

McDonald (1975) has found that pigeons can still orient in their training direction after sight of the sun itself is prevented by a sun shade apparatus worn by the bird. On the basis of his previous work (McDonald, 1968, 1972, 1973) he concludes this feat is a function of the pigeons differentially responding to changes in shadow parameters. Whether or not homing birds use shadows is an open question.

2) Olfactory cues. Prior to the 1960's olfaction was not considered important in birds. However, a series of anatomical and histological reports (Bang, 1960, 1965, 1966; Bang and Cobb, 1968) has served to emphasize the relatively

large size of the olfactory bulb in some species especially in procellariiformes. Neurophysiological evidence from pigeons and other species (Tucker, 1965; Henton, Smith and Tucker, 1966; Sieck and Wenzel, 1969; Wenzel and Sieck, 1973) confirms odour discrimination abilities similar to that in mammals. Behavioural data indicates that olfaction is important in the location of food by the Turkey Vulture, Cathartes aura and the Honey Guides, Indicator indicator, and I. minor (Stager, 1967); Kiwis, Apteryx (Wenzel and Sieck, 1973) and several procellariiformes (Leach's Storm Petrel, Wilson's Petrel, Oceanitis oceanicus, Manx Shearwater, and Sooty Shearwater, Puffinus griseus, Grubb, 1971, 1972, 1974). Grubb (1971, 1973, 1974) showed that Leach's Storm Petrel may employ olfactory cues to orient to nesting burrows at night. Thus as a "direct sensory cue" employable in Type I orienting, olfactory sources seem to have some importance.

Papi, Benvenuti and their coworkers have presented evidence suggesting the pigeon "map" is composed of associations between odours and wind directions. Olfactory nerve sectioning, (Benvenuti and Fiaschi, 1973) or obstruction of the nares (Snyder and Cheney, 1975) in experienced pigeons and restriction of olfactory experiences in young pigeons (Papi and Fiore, 1973) have impaired homing performances. Birds have returned to lofts where they had olfactory experiences but no visual experiences (Baldaccini, Benvenuti,

Fiaschi, Ioale, and Papi, 1974). Artificial deflection of wind directions at the home loft has resulted in predictable deflections in initial bearings in young pigeons (Papi, Ioale, Fiaschi, Benvenuti, and Baldaccini, 1974; Baldaccini, Benvenuti, Fiaschi and Papi, 1975).

Keeton (1974) and Keeton and Brown (1976) have questioned these results. Sectioning experiments and obstructing nares may influence homing independent of an olfaction effect (Keeton, 1974). Restricting and altering olfactory experiences at the home loft of both young and experienced pigeons had no effect on either initial orientations or homing performance (Keeton and Brown, 1976). At present the issue remains unresolved.

3) Auditory Cues. D'Arms and Griffin (1972) suggested naturally occurring sounds would be audible to heights at which migrating birds fly. Griffin and Hopkins (1974) and Griffin (1976) substantiate this and offer sound as a cue migrating birds might utilize to maintain orientation within mist or cloud. Homing birds as well may use sounds as Type I cues.

Infrasound has been postulated as a long range Type I information source (Griffin, 1969; Keeton, 1974). Psychophysiological studies employing pigeons (Kreithen and Keeton, 1974a) and Mallard Ducks (Lehner and Dennis, 1971) indicate that birds are sensitive to the very low pressure levels in

the infrasound spectrum. However use in either homing or migrating remains to be demonstrated.

4) Proprioceptive and Tactile Cues: Griffin (1969) suggested various roles for proprioceptive and tactile cues. Most of these were associated with detecting patterns of turbulence linked with particular weather configurations and were presented as sources of information by which a bird might maintain a heading in the absence of visual cues. That birds do respond to patterns of turbulence is suggested by the finding of migrating birds collecting at altitudes where winds are most favourable (Bruderer and Steidinger, 1972). Also passerines commonly maintain a downwind orientation during wind shifts (Able, 1974). In addition, sensitivity to the low pressure level changes reported earlier is of the order of magnitude to permit detection of barometric pressure changes (Lehner and Dennis, 1971; Kreithen and Keeton, 1974a). Such abilities would certainly assist a homing bird to hold its course and may even provide compass information in cases where the bird is released in the same weather system it was displaced in.

Barlow (in Keeton, 1974; Emlen, 1975) has postulated a form of inertial navigation in which the bird integrates all the twists and turns of the outward journey in order to compute the homeward direction. He suggested the vestibular apparatus and saccule as the appropriate sensory organs.

However, all efforts to provide evidence for this notion have failed (e.g. Griffin, 1940; Wallraff, 1972b; Schmidt-Koenig and Walcott, 1973; Keeton, 1974). Furthermore, it has been concluded that the information necessary for homing is gathered at the release site and not en route (Keeton, 1974). Probably inertial cues are only used for maintaining a chosen course (Emlen, 1975).

5) Geomagnetic Cues. There is good evidence for sensitivity to geomagnetic cues but the sensory systems involved are completely unknown.

In three species, applied magnetic fields have systematically disrupted orientation (Ring-billed Gulls, Larus delawarensis, Southern, 1969, 1971, 1972a, 1972b, 1974, 1975, 1976; Homing Pigeon, Keeton, 1971a, 1972, 1974; Herring Gull, Larus argentatus, Moore, 1975). In two of these, disruption in orientation has been correlated with naturally occurring magnetic field activity (Southern, 1969, 1971, 1972a, Keeton, Larkin and Windsor, 1974). With pigeons, this disruption occurred only under overcast skies when the sun was not visible (Keeton, 1971a, 1972, 1974).

Under visually cueless conditions caged migrants orient in the migratory direction appropriate to the season (European Robin, Erithacus rubecula, Wiltschko, Hock and Merkel, 1971; Wallraff, 1972a, Wiltschko, 1972; Wiltschko and Wiltschko, 1972; Garden Warbler, Sylvia borin, Wiltschko,

1974; Indigo Bunting, Emlen, 1975; Emlen, et.al., 1976). The relevant cue in each species was found to be the inclination of the magnetic field not its polarity, (Wiltchko and Wiltchko, 1972; Wiltchko, 1972, 1974; Emlen et. al., 1976). Polarity has not been as reliable a cue as inclination since the polarity of the earth's magnetic field has reversed several times during its history, (Freedman, 1973). Wiltchko et. al. (1971) and Wiltchko and Wiltchko (1975) add that European Robins, and three species of European warbler (genus Sylvia) orient according to the magnetic information when this conflicts with stellar information. In contrast Rabol (1975) reports continued orientation under starry and overcast skies when the magnetic field is disrupted for Garden Warblers, Redstarts, Phoenicurus phoenicurus, European Robins, and Blackcaps, Sylvia atricapilla. The basis for the contradiction of earlier studies is not clear (Rabol, 1975).

Attempts to condition pigeons to an operant task requiring discrimination of magnetic stimuli have not succeeded (Kreithen and Keeton, 1974c). However, changes in the magnetic field were perhaps too abrupt and not of a long enough duration for the pigeons to detect them (Keeton, 1974). Wiltchko (1972) reports that a three day acclimatization to new fields was necessary for proper orientation to occur.

Walcott (1972a,b, 1974) and Walcott and Green (1974) arranged small Helmholtz coils on pigeons' heads and necks

in such a manner that reversing the polarity of the battery supplying the current to the coils reversed the inclination of the magnetic field about the birds' heads. Under sun, all birds oriented correctly. Under overcast, the two groups oriented nonrandomly in directions separated by 180 degrees (Walcott and Green, 1974). Reversing the polarities of the properly oriented group on a second trial resulted in a reversal in orientation for half the group in spite of previous experience at that release site.

The findings of Walcott and Green coupled with those of Wiltchko and his colleagues strongly suggest that birds may actively employ geomagnetic cues when selecting flight directions.

Biology of Leach's Storm Petrel

(Class Aves; Order Procellariiforme; Family Hydrobatidae;
Genus Oceanodroma; Species leucorhoa; Subspecies leucorhoa)

Reviews of procellariiforme biology are found in Lack (1954, 1966, 1968) and Palmer (1962). Particular attention to Leach's Storm Petrel is paid by Gross (1935), Ainslie and Atkinson (1937), Palmer (1962), Wilbur (1969), Grubb (1971), Ainley, Morrell and Lewis (1974), and Ainley Lewis and Morrell (1976).

Leach's Storm Petrel at 30 - 54 grams (depending on the population) is the second largest member of the northern

hemisphere storm petrels, Hydrobatidae (Palmer, 1962). Like most other procellariiformes, it is an off-shore feeder, only coming to land to breed. During the winter, the birds generally migrate southward to the equatorial regions of the Atlantic or Pacific (Palmer, 1962; Crossin, 1974; Ainley, Morrell and Lewis, 1974; Ainley, Lewis and Morrell, 1976).

Lack (1968) has discussed the feeding ecology and breeding strategies of procellariiformes in general. The most important factor, the sparseness and unpredictability of their food supply (compared to that of inshore feeders and most terrestrial birds) is reflected in the following features of their biology:

(1) Lower Metabolism. Lower basal temperatures and slow growth rates indicate a low metabolism throughout the order (Lack, 1968; Warham, 1971). A lowered metabolism requires less food to maintain it. The slow growth rate is reflected in the time required from egg laying to fledging, 104-112 days (Huntington in Palmer, 1962). Incubation lasts 41 to 42 days and may be extended by temporary desertion during the incubation period. Such desertions can last five or more days. The resistance of the embryo to chilling has been noted in many procellariiforme eggs (Gross, 1935; Roberts, 1940; Matthews, 1954b; Davis, 1957; Pefaur, 1974; and others). Presumably, the low metabolic rate and large egg size (20% of body weight in Leach's Storm Petrel, Lack

1968) account for this attribute.

Lowered metabolism permits longer incubation shifts. Thus the average length of time one Leach's Storm Petrel incubates before being relieved by its mate is 2.71 days. This varies from one to at least five days. (Wilbur, 1969). Weight loss, while incubating, is reported to be 2.2 grams per day (Huntington in Billings, 1968).

Growth post-hatch is also slow necessitating 63-70 days to fledging (Huntington in Palmer, 1962). Brooding lasts from one to three days with only rare daytime stay-overs thereafter (Palmer, 1962). The chicks are fed at best twice a given night but usually only once and frequently nights are missed (Ainslie and Atkinson, 1937; Palmer, 1962). In other high latitude hydrobatidae (e.g. Pelagodroma marina, Richdale, 1943a, 1943b, 1965; Hydrobates pelagicus, Davis 1957; Fregatta tropica, Beck and Brown, 1972) the frequency of feeds is initially high and the amount of food delivered is low. Within a week to two weeks post hatch, the chick is able to accommodate as much food as the parents can bring. Consequently the frequency of visits decreases somewhat while the amount of food delivered per feed increases. A similar pattern is probable for Leach's Storm Petrel. As fledging approaches, both the frequency of visits and the amount of food decline and the parents may cease visiting the chick 1-3 days before it actually fledges (Huntington, Pers. Comm.). Associated with this is a decline in weight,

completion of feather growth and sojourns outside the burrow for wing exercising (Gröss, 1935; Huntington in Palmer, 1962).

(2) Efficient Flight Surfaces. All procellariiformes (except the prions, Richdale, 1965) have efficient long wing surfaces permitting soaring flight in light airs and further reducing energy requirements (Lack, 1968).

(3) Keen Olfaction. A pronounced feature throughout the order is the tube nose. The prominence of the external nares, plus the high olfactory bulb to brain ratios (Bang, 1960, 1965, 1966; Bang and Cobb, 1968) suggest an important role for olfaction in the order as a whole. Anecdotal and behavioral data suggest that food sources may be located via olfaction (Grubb, 1971, 1972) and presumably selection has favoured such anatomically large olfactory regions for this reason.

(4) Delayed Maturity. In Leach's Storm Petrel, most young birds do not visit the breeding colony until the age of three while breeding for the majority begins at five (Huntington and Burt, 1972). It is thought that such a delay allows prebreeders to learn the best foraging areas and select their nest sites and mates (Lack, 1968).

(5) One Egg Clutch. No procellariiformes lay more than one egg. Twinning experiments in several species including Leach's Storm Petrel (Huntington, 1963) reveal that usually parents cannot provide enough food for more than one young. In addition, the laying of replacement clutches in

the event of egg loss, though documented, is quite rare (Wilbur, 1969; Beck and Brown, 1972).

(6) Longevity. Associated with the one egg clutch and delayed maturity, both of which drastically reduce productivity per breeding pair, is an increased longevity. Three birds, banded while breeding are known to have survived 16 years. Since, the minimum age of first breeding is two, their minimum age was 18 years (Huntington and Burt, 1972).

Little is known directly of the feeding ecology of Leach's Storm Petrel. They are surface feeders limited to catching organisms in the top few centimetres of the sea and because of the birds' size, prey over 6 cm in length are probably too large (Huntington, 1963; Ashmole, 1972). It seems likely that Leach's Petrel take advantage of the nocturnal vertical migrations to the surface of many zooplankton and thus feed mainly at night. Such a strategy has been documented in several petrels (Imber, 1973, 1976).

Next to the type of food supply, the most important selection pressure has been predation. Leach's Storm Petrel is highly susceptible to any mammalian carnivore. Consequently the birds breed in colonies only on inaccessible islands (Gross, 1935; Palmer, 1962; Wilbur, 1969).

Because of their small size, they are victimized by avian predators such as the Great Black-backed Gull, Larus marinus, and the Herring Gull, (Gross, 1935). Adaptations

limiting losses are nocturnality at the breeding ground and nesting in burrows.

Homing in Leach's Storm Petrel

Previously, four homing studies have been conducted with O. leucorhoa, Griffin (1940), Griffin and Goldsmith (1955), Billings (1968), and Grubb (1971, 1974).

Griffin (1940) displaced petrels different distances and directions from Kent Island, New Brunswick. Some groups were subjected to a few seconds of an intense electromagnetic field, others were rotated on turntables during the displacement, while the remaining served as controls. The return times of the birds were only marginally affected by distance and not affected by either the electromagnetic or turntable treatments. Griffin concluded that petrels did not wander randomly in a search for their breeding island; otherwise, return times should have increased as a function of distance.

He also concluded that neither geomagnetic nor inertial cues were necessary for homing. Though these cues may not be essential, his data do not indicate that these factors cannot aid a homing bird when they are available.

Because birds were displaced over the ocean and homed successfully, Griffin inferred topographical cues and therefore vision were not important for homing petrels. However,

new evidence, described earlier, indicates there are more sources of visual information than topographical features (Keeton, 1974; Emlen, 1975).

Griffin also freed birds on each side of the 29 km wide isthmus joining Nova Scotia to New Brunswick. Those released on the Bay of Fundy side had 192 km to fly directly over water to reach Kent Island. Those released on the Northumberland Strait side had either 258 km to fly if they went overland and down the Bay or else 926 km if they remained over water and flew around Nova Scotia. Since all homed in approximately the same amount of time, Griffin concluded that the Northumberland Strait birds homed overland, a feat indicative of Type II homing (Griffin, 1940).

A scrutiny of Griffin's data reveals that petrels' mean number of km per day homing rates increase as the distance of displacement increases. Thus it is possible that the Northumberland Strait birds speedily flew the all water route around Nova Scotia while the other birds dallied down the Bay of Fundy. This is supported by the fact that all rates calculated on the basis of the longer route are well within petrel's capabilities (Billings, 1968).

Oriented bearings at the release site could provide evidence of the route taken by petrels. However, attempts at gathering vanishing bearings with Leach's Storm Petrel have either led to a random scatter (Griffin and Goldsmith,

1955), downwind drifting (Griffin and Goldsmith 1955; Billings, 1968) or orientation to the nearest body of water (Billings, 1968). Successful homers do not seem to orient homeward at the release site (Griffin and Goldsmith, 1955; Billings, 1968). In addition the reliability of the measure was questioned because of the difficulty of following a bird as small as a petrel with its butterfly style flight (Griffin and Goldsmith, 1955).

Billings (1968) replicated the trans-isthmus release, extending the design by using several different pairs of sites each offering the experimental group a choice of a shorter overland route or a longer all water route. Her overall homing times were much shorter than Griffin's. This was attributable to the reduced amount of time the birds were held in captivity (Billings, 1968). Differences between the experimentals and controls were not significant. She concluded that her experimental birds took the overland route. However, her data portray the same distance-homing rate relationship as Griffin's and are therefore subject to the same restrictions.

Two points apply to both sets of data: First, in the critical transisthmus releases, only small numbers of birds homed, thus limiting the generality of any conclusions. Secondly the arguments assume that birds away equal times fly equal distances, and furthermore, that these distances are

related to the distance of displacement. However, beyond the bare minimum required to home, the distances a displaced petrel travels are largely unknown. This is underscored by the fact that birds released on the home island (Griffin, 1940) took as long to return to their burrows as those released 752 airline km away.

Two other releases are of note. Billings displaced seven birds to England. Four returned. Griffin and Goldsmith released 22 petrels more than 32 km inland. Of these five returned within five days after which checking was discontinued. Both displacements are important in that they confirm sophisticated orientational abilities in Leach's Storm Petrel. However, what cues the birds relied on and how these cues were used remained open to question.

Grubb (1971, 1973, 1974) demonstrated that petrels 1) are attracted to food odours at sea; 2) fly upwind to their colony; 3) land downwind and walk upwind to their burrows; 4) turn towards their own versus other nest material in a Y-maze olfactorium, and 5) fail to home to their burrows when olfactorily impaired. These results suggest olfactory cues are used at close range as direct sensory cues (Type I orienting). It may be possible for petrels to associate specific smells with particular places. If so, smell could be used in the "landmark" sense and thus could aid the birds in orienting at distances beyond which the smell of their colony extends.

A separate piece of evidence useful for future work was the control data for the olfactory impairment experiments (Grubb, 1971, 1974). Of 35 birds that were collected and released unharmed, 32 (91%) returned taking from one hour to eight days to do so. Since these birds were released while on their home island, varying navigational abilities is not the reason for the discrepancy in return times.

Homing is a complex behavior; its performance depends as much on motivational factors as on orientational skills (Keeton, 1974; Ralph and Mewaldt, 1976). In procellariiformes, weight is a likely indicator of motivational state. This may be a function of fat reserves which are highest early in the season (Matthews, 1954a; Hatch, 1974) or due to recency of return from foraging expeditions (Billings, 1968). Billings divided her birds into fast and slow groups of homers and found that faster homers were significantly heavier when first captured prior to displacement than slow homers.

In summary, Leach's Storm Petrel appear to be a good species for the study of homing. As a wide-ranging forager, and as a medium distant migrant it has well developed navigation skills. Because it is a colonial nester, large numbers are accessible at a time and they are easy to trap and readily located as a result of their burrowing habits. Resistance of the egg to chilling and the extended nature of their incubation shifts reduce the probability that displacing an incubating adult will have a detrimental effect.

Furthermore, Leach's Storm Petrel is a proven homer. Olfactory information may provide near range orientational cues but cues employed at greater distances are unknown. Weight is implicated as an indicator of motivational status. Consequently, the present series of displacements were designed to determine the Type of orienting performed by Leach's Storm Petrel and to shed more light on the motivational factors which may influence homing-times.

The Study Site

Middle Lawn Island ($46^{\circ}55'N$, $55^{\circ}36'W$, approximately 500m x 300m, elevation about 75m) was selected as the study site. Topographically the island has three features: rocky cliffs 20-30m high ring it; a sloping plain comprises the north half; a large hill forms the south half. It is located in Placentia Bay, Newfoundland near the southern end of the Burin Peninsula.

A census in the spring of 1975 revealed upwards of 26,000 active burrows of Leach's Storm Petrel (Lien, Pers. Comm.). Other birds breeding in small numbers included Black Guillemots, Cepphus grylle, Great Black-backed Gulls, and a few unidentified sparrows and warblers. The only mammals were sheep. The flock in 1975 numbered 40 during July but was trimmed to twenty in August. In 1976, only twenty were pastured on Middle Lawn Island.

Three relatively distinct types of vegetation occurred, grass, ferns, and irises. Usually the iris was associated with the wettest ground while grass and ferns covered the better drained areas. The petrels burrowed virtually everywhere though the greatest densities occurred in ferns and grass which were predominant on the summit and the north and northwest slopes of the main hill.

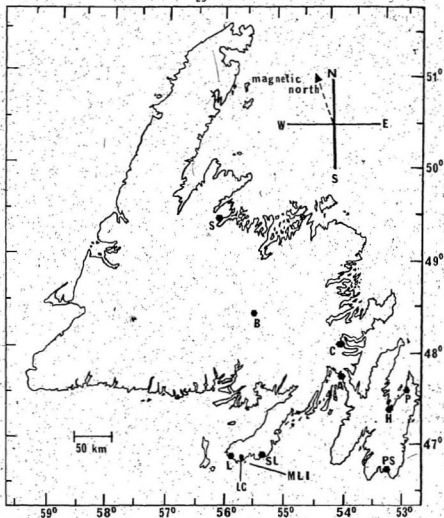
Displacement 1, 1975

Billings (1968) and Griffin (1940), on the basis of a limited number of returned birds suggested petrels may have flown over an 18 mile wide stretch of land. Such a result would indicate Type II orienting ability. A replication of their results was attempted using different release sites and a different population of birds. Clarenville is 186 km from Middle Lawn Island assuming birds fly across the narrowest portion of the isthmus that joins the Avalon Peninsula to Newfoundland. An all water route around the Avalon is about 400 km. Arnold's Cove to Middle Lawn Island is 160 km over water (see Figure 1). After Grubb (1971, 1974) a control group was released locally to assess and control for the possible influence of motivational factors.

Method

Subjects

Twenty-nine adult Leach's Storm Petrels were taken from their burrows on Middle Lawn Island. Twenty-five birds



- | | |
|--------------------------|--------------------------|
| A - Arnold's Cove | MLI - Middle Lawn Island |
| B - Bay d'Espoir Highway | P - Portugal Cove |
| C - Clarenville | PS - Portugal Cove South |
| H - Holyrood | S - Springdale |
| L - Lories | SL - St. Lawrence |
| LC - Lord's Cove | |

Figure 1. Locations of release sites in Displacements 1-5, 1975, 1976.

were found singly incubating eggs. Two were found together in a burrow with an egg and two were found in a burrow without an egg.

Apparatus

Aluminum bands obtained from the Canadian Wildlife Service were used for marking and identifying individual petrels. Birds were transported in carrying cases (34 cm long x 9 cm diameter) of polyvinyl chloride plastic pipe. One end was screened, the other was covered by a wooden door secured by elastic bands. Numbered wooden stakes were used to mark burrows.

Procedure

i. Collection. On 30 July, 1975, between 13:00 and 16:00 hours, burrows in a well populated area of the colony were entered by hand. When a bird or birds were located, they were banded and placed in a carrying case along with a small amount of peat from their burrow. A stake was placed by the burrow and the burrow entrance was covered by a straw lattice. Nineteen birds were collected, 10 were designated for Clarenville and 9 for Arnold's Cove including 1 pair to each site. Ten control birds were collected in the same manner 31 July between 17:30 and 18:30.

ii. Displacement. Birds were transported to Lord's Cove by boat and then by car to the release sites. The

Clarenville release occurred first between 23:32 and 23:42 hours, 30 July, while the Arnold's Cove release took place at 00:35 to 00:42 hours, 31 July. Birds were singly tossed towards each of the 4 major compass points in succession. Control birds were released starting 21:30, 31 July. Birds were singly tossed from beside their burrows.

iii Release Site and Weather Descriptions.

a) Clarenville. The release took place at a viewing site on the Trans Canada Highway 2.7 km south of the turn off to Clarenville. The site overlooked the North West Arm of Trinity Bay. Behind the site across the road to the west was a high cliff. Winds were light, 0-20 km/h from 180° ; visibility was unlimited and cloud cover was estimated at 10%.

b) Arnold's Cove. This release site was on a spit of land jutting into Placentia Bay. From the car top, water was just visible at 180° and 360° but a slight hill at 270° obscured sight of water in that direction. Winds were light, 10-16 km/h from 180° . Visibility was restricted by a thick coastal fog to 150 m. Cloud cover could not be determined.

c) Middle Lawn Island. The release occurred on the plain 30 metres north of the base of the main hill. Winds were 0-4 km/h, variable in direction. Visibility ranged from 200 m to 4 km because of coastal fog patches. Cloud

cover was estimated at 90%.

iv Burrow Checks. Checks for returned birds were carried out once during the day and three times each night commencing the night of the release. Whenever a lattice was disturbed or thought to be disturbed, the burrow was entered and explored by hand. This procedure was continued for 8 days. Daytime checks alone occurred 8-10 August. Because the lattices were frequently disturbed but no homers were caught, night checks were reinstituted 11-16 August. Daily checks continued until 7 September.

Results

Weather Conditions

During the two weeks following the displacement, generally fair weather prevailed; winds were light to moderate (0-30 km/h).

Success and Return Times

Both homing success and return time are illustrated in Figure 2. The eight (80%) returning control birds averaged 99.38 h. Four birds (44%) of the Arnold's Cove group homed in a mean time of 70.25 h. Seven (70%) returned from Clarenville in $\bar{X} = 111.14$ h. In spite of the apparent differences between means, there was no significance between those differing the most (Clarenville-Arnold's Cove, $t = 1.27$, $df=9$; $p>10$, one-tailed test: Control - Arnold's

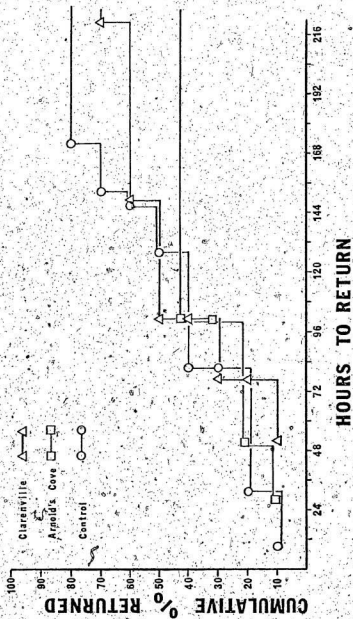


Figure 2. Cumulative percent returned and hours to return of Leach's Storm Petrels in Displacement 1, 1975, Arnold's Cove - Clarendville.

Cove, $t = .89$, $df = 10$, $p > .15$, one-tailed test). In addition, scoring returners (1) and non-returners (0) and then comparing the most successful group, Controls, to the least successful group, Arnold's Cove, yielded no significance ($t = 1.63$, $df = 17$, $.10 > p > .05$).

On the assumption that the four birds returning from Arnold's Cove were the best homers, it was decided to compare these to the best four in the other groups. The best four Controls ($\bar{X} = 49.5$ h) were significantly faster than Arnold's Cove birds ($\bar{X} = 70.25$ h, $t = 43.35$, $df = 3$, $p < .0005$, one-tailed test direct difference method: Student's t Ratio, Runyon and Haber, 1971), and the Clarenville best four ($\bar{X} = 71.95$ h, $t = 2.4$, $p < .05$, one-tailed test). Arnold's Cove and Clarenville best fours were not significantly different ($t = .55$, $p > .25$, one-tailed test).

Because seven birds returned from Clarenville, their times were compared via the direct difference method with the first seven controls. In spite of the apparent difference in means, (Control = 89.14 h, Clarenville = 111.14 h), significance was only approached, not attained. ($t = 1.75$, $df = 6$, $.10 > p > .05$, one-tailed test).

Of the subjects which were members of a pair at collection, none returned.

Discussion

The results lend themselves to several interpretations. First the longer mean time of the Clarendville group may indicate they flew the all water route. The reason for the lack of significance would then be attributed to the small sample resulting from the poor success of the Arnold's Cove birds. This could be a function of the fog at the release site.

Secondly, the lack of significance between group means may be indicative of trans-isthmus homing on the part of the Clarendville birds. However, generally long return times mitigate against such a conclusion.

Thirdly, perhaps just the fastest Clarendville birds crossed the isthmus while the slow ones circled the Avalon Peninsula. This is suggested by the similarity in times of the best four homers of the Clarendville birds and the best four of the Arnold's Cove group.

Unfortunately, even if birds did cross the isthmus, Type II orienting may still be questioned on the grounds that the distance across, less than 5 km, is not great enough to prevent detection of the opposite shore. To prevent this different sites would be needed.

Finally, the wide variation in homing time implicates varying motivational levels, as well as navigational skills.

Focusing on the control bird data illuminates this point. These birds took from a few hours to over seven days to return, a finding consistent with Griffin (1940) and Grubb (1971). Identification of a motivational indicator might help account for some of this variance and thus permit more accurate statements about homing routes.

Displacement 2, 1975

In Displacement 2, there were three objectives. First, Grubb's work (1971, 1973, 1974) suggests that petrels within downwind range of olfactory cues emanating from their home island would be at an advantage over upwind birds. This hypothesis was tested by displacing two groups of birds, one upwind to Lories and one downwind to St. Lawrence. Both sites are within 20 km of Middle Lawn Island (see Figure 1). Secondly, it was of interest to test, a priori, the effect of collection weight on homing times (after Billings, 1968). Thirdly, it seemed important to determine if Leach's Storm Petrel would display nonrandom orientation at the release site. In lieu of vanishing bearings it was decided to use orientation activity chambers (Emlen and Emlen, 1966).

Method

Subjects

Twenty-eight Leach's Storm Petrel adults were used. Of these, 25 were incubating eggs, 1 was brooding a chick, and 2 were found as a pair in a burrow without an egg. These last three were among the displaced birds.

Apparatus

Carrying cases, stakes and bands, as previously described, were used. Weighing was done with a triple beam O'Haus balance, Model 2610. A Silva compass was used to determine directions. The orientation activity chamber was modelled after that of Emlen and Emlen (1966). Each one consisted of a desk blotter cut and stapled to form a cone, the outer rim of which lies flush with the rim of the supporting tub. The small end of the cone is open and centered by an inner pan. Stamp pad ink is daubed onto a pad in the inner pan. A heavy wire screen bent over the edges of the tub retains the subject. Activity in the chamber was recorded by ink marks left by the birds feet and tail (see Figure 3).

Procedure

i Collection. Birds were collected from a densely populated area of the colony as before. Collection of displaced birds (n=20) occurred 9 August, 1975 between



Figure 3. An activity chamber in use with the wire screen top removed. The bird in this instance is a fully feathered Leach's Storm Petrels chick.

16:00 and 18:30 hours. At 18:30 all birds were taken to camp, weighed, then divided into heavy (50 grams and over) and light (under 50 g) groups. One half of each weight group was randomly assigned to St. Lawrence, the other half went to Lories.

Control birds (n=8) were collected 11 August from another area of the colony. At 18:00 hours they were carried to camp, weighed and designated as heavy or light according to the above criterion.

ii Displacement. At 19:30, 9 August, the Lories and St. Lawrence birds were transported by boat to Lord's Cove and by car to their respective sites simultaneously. All birds were placed in activity chambers at 21:30 hours and released directly from the chambers at 23:00 hours. They were tossed in the four major compass directions. Control birds were subjected to the same procedure at the same time only on 11 August on Middle Lawn Island.

iii Orientation Activity Chamber Procedure. To reduce confounding due to proximity and olfactory cues, the chambers were placed 5 m apart in a straight line perpendicular to the wind direction. The chambers were levelled by eye. A carrying case containing one bird was placed by each chamber. Then the pads in the inner centering pans were inked. Using the compass, magnetic north was determined and marked at the appropriate spot on the outside of the tub. The blotter cone was inserted, its north mark on its

outer rim being lined up with the tub's north mark. All the birds were placed in the chambers within a 5 min. period and the experimenters withdrew from the area for 90 min. At the end of the trial, each chamber was approached as quietly as possible and the bird's final heading was noted. After the bird was removed, this was marked on the inside of the cone.

Three raters independently scored the cones for major activity direction and activity level. A measure of agreement was computed as an indication of the reliability of the scoring procedure. (See Appendix A for full details).

iv Release Site and Weather Descriptions.

a) St. Lawrence. The location was on the Middle Head Lighthouse point, 100 m west off the road, about 300 m from the lightkeeper's houses on the point and approximately 200 m from the nearest sea. At 21:30, weather was calm: wind, 3-8 km/h from 260° - 280° ; temperature, 15°C ; visibility, unlimited; cloud cover, 10%. By 23:00 hours wind speed had increased slightly to 8-13 km/h.

b) Lories. This site was about .8 km from the main road, 100 m from the sea on a flat bog plain. It was located 17 km by road, west of Lord's Cove. Weather was as follows: temperature, 15°C ; wind, 10-13 km/h from 270° ; cloud cover, 40%; visibility, unlimited. Conditions did

not change during the trial.

c) Middle Lawn Island. The chambers were on the plain, north west of the main hill and ran in a line 50 m from the ocean perpendicular to the wind. Weather conditions follow: temperature, 20°C; wind, 6-8 km/h from 125°; visibility, limited to 100 m by fog. No sky could be seen through the fog.

v Burrow Checks. Homers were checked for during the day, 10 August and at 00:30 and 03:00, 11 August. From then on checks were once during the day and three times at night, 23:00, 01:00, and 03:00. Since birds never arrived prior to 21:00 nor after 05:00, arrival times were accurate within 2 hours assuming the bird was captured on its first visit to the burrow. This schedule was continued until 26 August, 1975, after which one check occurred nightly at 01:00 until 7 September. Checks for control birds began at 23:30, 11 August and occurred thereafter at the same time as those for displaced birds.

Results

Weather Conditions

The weather remained calm until 14 August. Winds never exceeded 25 km/h and were mostly under 10 km/h. All homing birds returned during this time. An electrical storm bringing winds gusting to 50 km/h from the SE on

15 August may have deterred potential homers. However weather conditions were favourable for the next three days.

Success and Return Times

Homing success and return time are depicted in Figure 4. Three control birds (38% of those displaced) averaged 26.9 h to return. Six Lories birds (60%) returned in $\bar{X} = 75.4$ h. Eight of the St. Lawrence group (80%) homed in $\bar{X} = 63.8$ h. Three t-tests (each testing for differences between the means of two independent samples) were run comparing the return times of successful homers from the three possible pairs of release locations. None were significant. Scoring homers (1) and non returners (0) and then comparing the groups with independent t-tests reveals that the St. Lawrence birds were more successful than the controls (80% vs 38%, $t = 1.92$, $df = 16$, $p < .05$, one-tailed test), but that Lories and the controls did not differ (60% vs 38%, $t = .92$, $df = 16$, $p > .10$, one tailed test).

The birds in each group were then ranked lowest to highest according to their return times. Using the direct difference method (i.e. a t-test for two correlated samples) student's t ratios were calculated on the differences in return times between equally ranked birds. Thus the first St. Lawrence homer's return time was compared

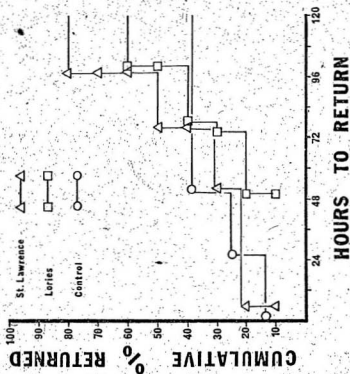


Figure 4. Cumulative percent returned and hours to return of Leach's Storm Petrels in Displacement 2, 1975, Lories - St. Lawrence.

to the first Lories homer's and the second St. Lawrence bird's to the 2nd homer's from Lories, etc., until one of the groups was exhausted. Remaining birds in the larger group were then excluded from the analysis.

This treatment of the data yielded the following results. St. Lawrence birds returned significantly sooner than Lories birds ($n = 6$ pairs, $df = 5$, $t = 4.87$, $p < .025$, one-tailed test). Control birds homed sooner than the Lories birds ($n = 3$ pairs, $df = 2$, $t = 3.75$, $p < .05$, one-tailed test). St. Lawrence birds and controls did not differ ($n = 3$ pairs, $df = 2$, $t = .69$, $p < .25$, one-tailed test).

In terms of the breeding status the composition of the population of homers can be described as follows: birds on eggs, 13/17 (76%) displaced birds, 3/8 (38%) control birds; members of a pair 0/2 (0%); birds brooding a chick, 1/1 (100%).

Weight and Return Time

The mean weight of the heavy group was 55.51 grams, the mean weight of the light group was 46.63 grams. The return times of the heavy birds were compared to return times of the light birds collapsed across all three locations. Heavy birds returned significantly sooner than light birds (heavy $\bar{X} = 47.14$ h, light $\bar{X} = 87.42$ h, $df = 15$, $t = 2.70$, $p < .01$, one-tailed test). In the displaced

groups 9/10 (90%) heavy birds returned while only 5/10 (50%) light birds returned. In the control group, however, there was only 1 light bird and it returned. Only 2/7 (29%) heavy controls returned. With one exception, heavy birds from a particular group homed before the light birds within that group.

Orientation Activity Chamber Results The raters agreed 79% of the time over the three groups in their judgements of major activity direction and 89% of the time in their judgements of activity level. Two birds' (1 from Lories, 1 from St. Lawrence) major activity scores were not included because the raters considered their activity as random. An additional Lories bird's major activity score was excluded on the basis of insufficient activity during the trial.

The major activity directions and final headings are illustrated in Figure 5. On neither of these measures were the orientations clustered significantly ($p > .10$, Rayleigh test, Batschelet, 1972) nor were the displaced birds significantly oriented homeward ($U < 1.1$, $n = 10$, $p > .10$, V test, Batschelet, 1972). However, a Watson's and William's test (Batschelet, 1972) comparing all three samples on final heading scores was significant ($F = 3.43$, $df = 2/25$, $p < .05$). The same test applied to the major activity direction score approached significance ($F = 3.07$, $df = 2/22$, $.10 > p > .05$). The direction of the mean

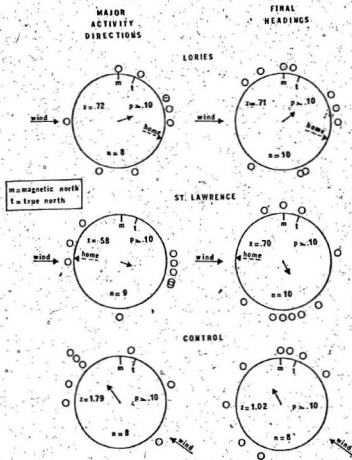


Figure 5. Major activity directions and final headings of the Displacement 2 activity chamber test. Arrows in the centre of each circle depict the direction and strength of the mean vector for that sample.

vectors in Figure 5 suggested that this result ought to be accounted for by the differences between control and the displaced groups. A series of two sample Watson's and William's test confirmed this. (see Table I). The most significant difference appeared between St. Lawrence and the control birds. Interestingly, the differences between St. Lawrence and Lories were the smallest.

Figure 5 suggests that perhaps these differences could be accounted for by wind direction. Thus, all scores were plotted with reference to the direction the wind was blowing on the night of their particular trial (see Figure 6). A V test was run with the prediction that the birds were orienting downwind (or 180° from the reference point). Major activity direction was significant ($p < .05$, V test) while final headings were not ($.10 > p > .05$, V test).

Discussion

There was no clear homeward orientation evident in the activity chamber tests. Rather the birds seemed to be responding to wind direction by orienting in line with it. Such a finding agrees with the observation that many migrating passerines orient downwind (Able, 1974). In the present instance, downwind orientation ought to have conferred a homing advantage to the Lories birds.

However, t-tests for independent samples yielded no

Table 1.

Summary of Watson's and William's Tests (Batschelet, 1972)
 Comparing Release Sites on Major Activity Direction and
 Final Headings.

Lories vs St. Lawrence

Major Activity Direction $F=2.27$, $df=1/15$, $p>.25$

Final Orientation $F=2.37$, $df=1/18$, $.25>p>.10$

Lories vs Control

Major Activity Direction $F=3.40$, $df=1/14$, $.10>p>.05$

Final Orientation $F=1.6$, $df=1/16$, $.25>p>.10$

St. Lawrence vs Control

Major Activity Direction $F=5.05$, $df=1/15$, $p<.05$

Final Orientation $F=6.79$, $df=1/16$, $p<.05$

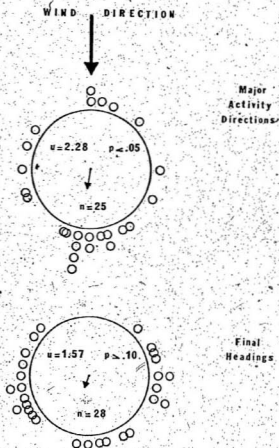


Figure 6. Major activity directions and final headings of the Displacement 2 activity chamber test plotted with reference to wind direction.

significant differences between release sites. This is readily attributable to the wide range in scores for all groups. Similar ranges are also apparent in Displacement 1 and this range may represent a performance scale. In general, the data indicated that scale position accounts for a greater proportion of variance in return time than group membership and may mask any group membership effect. Thus controlling for scale position may allow an assessment of membership effect. Essentially this is performed by the use of t-tests for correlated samples -- the assumption being that birds of equal rank are of equal homing ability. Thus any systematic difference between equally ranked birds of different groups would suggest some environmental influence.

The t-test for correlated samples indicated that St. Lawrence birds and controls did not differ but that both of these homed sooner than Lories birds. This finding agrees with the prediction that downwind birds (St. Lawrence group) would home sooner than upwind birds (Lories group) and thus supports the use of olfactory cues by Leach's Petrel. Furthermore it suggests that in a homing situation, olfactory cues take precedence over wind direction cues; i.e. even though the birds oriented downwind in the activity chambers they homed better flying upwind. Meanwhile, in an escape situation, (as in the activity chambers) the cue of prime importance appears to be wind direction.

The low success rate of the control group, 38%, is troublesome. Griffin (1940) reports a decline in homing success as the season progresses and suggests advanced breeders are less motivated to return. Possibly the area of the colony the controls were selected from was more advanced in the breeding cycle. At any rate another group of control birds, gathered from another area of the colony and released at the same time fared far better -- 65% returned. Thus neither experimental technique, nor weather conditions are likely contributors to the low rate.

The weight hypothesis was clearly confirmed. Heavy birds at collection home sooner than light birds. The effect here was stronger than that obtained by Billings (1968). This may be due in part to the fact she truncated her weight range by selecting for her displacements birds that had been incubating 48 h or less.

Displacement 3, 1975

In an effort to obtain less equivocal results than in Displacement 1, a second transisthmus release was undertaken. To avoid the fog at Arnold's Cove and to increase the distance of the shorter overland route, two new sites were chosen. These were Portugal Cove South and Holyrood (see Figure 1). From Portugal Cove South to Middle Lawn Island by water is approximately 184 km. From

Holyrood there are at least four potential routes: 1) all water around the Avalon Peninsula, 403 km; 2) direct airline route, 195 km; 3) overland directly to Placentia Bay and then straight to the island, 199 km; 4) shortest overland route, 33 km, to St. Mary's Bay and then by water totaling 218 km. Thus petrels displaced to Holyrood must either fly over at least 33 km of land or go twice as far to home as birds released from Portugal Cove South.

Heavier petrels home sooner than lighter petrels (Displacement 1, Billings, 1968). Billings thought that differences in weight and therefore differences in homing performance were a function of recency of return from foraging. However all her displaced birds were within 48 h from foraging and differences in weight in her birds may have been due to differences in fat reserves or sheer physical size. To decide the issue birds were weighed on return as well as at collection. If recency of return is the prime reason for weight differences, then heavier birds, homing sooner, ought to have less foraging time and thus lose weight en route. Light birds would gain weight. If size is important, then heavier birds ought to return weighing more than lighter birds. In addition, if physical size was the sole factor, then there should be little weight change between collection and return.

Method

Subjects

Twenty-nine Leach's Storm Petrel adults were collected. Twenty-six were found incubating, two were found as a pair with no egg and one was found alone. Of these eight incubators and the alone bird were controls.

Apparatus

Carrying cases, stakes, compass and triple beam balance, as previously described, were used.

Procedure

i Collection. Displaced birds were collected starting 15:00, 10 August, 1975. Nine controls were gathered 12 August, from an area 20 m from the displaced birds. All burrows were staked and latticed. Subjects were banded, weighed and housed in individual carrying cases as before. Birds were divided into two groups on the basis of weight, heavy and light. Of the experimental birds, half of each weight group was randomly assigned to each displacement site. Thus five heavy birds and five light birds went to each site.

ii Displacement. Transport to Lord's Cove was completed by 19:00, 10 August. Birds were released in Holyrood at 00:20, 11 August and from Portugal Cove South at 03:00, 12 August. Control birds were released at 24:00,

12 August, 60 m from their burrows. One petrel did not fly. It was tossed three times. Not being certain of its condition, it was released into its burrow and excluded from further consideration¹.

iii Release Site and Weather Descriptions.

a) Holyrood. Birds were released 200 m north from the Conception Bay Highway junction with the Trans Canada Highway on a beach 10 m from the water. Weather conditions follow: temperature, 15°C; wind, 0-2 km/h from varying directions; visibility, unlimited; cloud cover, 20%.

b) Portugal Cove South. This release took place beside the community wharf on a beach 20 m from the water. Weather follows: temperature, 14°C; wind, 0-2 km/h from varying directions; visibility varied from 100 to 500 metres due to fog patches; cloud cover, 10%.

c) Middle Lawn Island. The release occurred on the plain north of the hill. Weather conditions were generally calm: temperature, 18°C; wind, 0-4 km/h from 90°; visibility, 100 metres in a thick fog; cloud cover could not be estimated.

iv Burrow Checks. For displaced birds, all

¹This bird was recaptured in 1976 in the same burrow, alive, well and incubating an egg.

burrows were checked once daily beginning during the day 11 August, and three times nightly (23:00, 01:00, 03:00) until 26 August. Thereafter one check occurred nightly at 01:00 until 7 September. Control birds were checked for 01:00 and 03:00, 13 August. From then on checks occurred at the same time as those for displaced birds. All homers were weighed before being returned to their burrows.

Results

Weather Conditions

Weather conditions varied between 11 August and 20-21 August, the last night a homer was recaptured. Winds remained calm 10-14 August. On 15 August a minor disturbance resulted in winds 10-50 km/h from the SE. By evening, this had subsided, as a ridge of high pressure approached. The following low resulted in a steady 30-40 km/h winds from the SE during 18-19 August. As the centre of the low passed, the winds dropped to 25 km/h and shifted to SW bringing fair weather 19 August through the day of 20 August. The night of 20-21 August ushered through the high pressure ridge. This was associated with several squalls with winds gusting to 50 km/h. Between squalls winds remained about 25 km/h, the skies were clear and visibility unlimited.

Success and Return Time

Homing success and return time are illustrated in

Figure 7. Eight (80%) of the Portugal Cove South petrels returned in an average of 83 h. Seven (70%) of the birds displaced to Holyrood homed in $\bar{X} = 52$ h. Of the controls, 5/8 released (63%) returned in $\bar{X} = 89$ h. Neither t-tests for independent means nor t-tests for correlated samples indicated there was any difference between groups in time to return (see Table 2). Success was also equivalent.

Of the pair of birds collected one returned. Nineteen of twenty-seven (70%) of the incubating birds homed.

Weight and Return Time

Collection weights of displaced birds were as follows: heavy birds, $n = 10$, $\bar{X} = 62.8$ g; light birds, $n = 10$, $\bar{X} = 51.9$ g. Controls weighed \bar{X} - heavy = 57.8 g, $n = 4$, and \bar{X} - light = 52.6 g, $n = 4$. Success did not differ between light and heavy groups, 11/14 (79%) and 9/14 (64%) returned respectively.

As before, heavy birds returned sooner than light birds (\bar{X} - heavy = 29.22 h, \bar{X} - light = 108.18 h, $t = -3.69$, $df = 18$, $p < .005$, one-tailed test).

Two homers from Portugal Cove South were not weighed at return. One was a heavy bird, one was a light bird. Thus both collection and return weights were available for eight heavy's and 10 light's. Heavy petrels lost weight between collection, $\bar{X} = 60.8$ g, and return, $\bar{X} = 55.04$ g, (correlated $t = 6.01$, $df = 7$, $p < .001$, two tailed test).

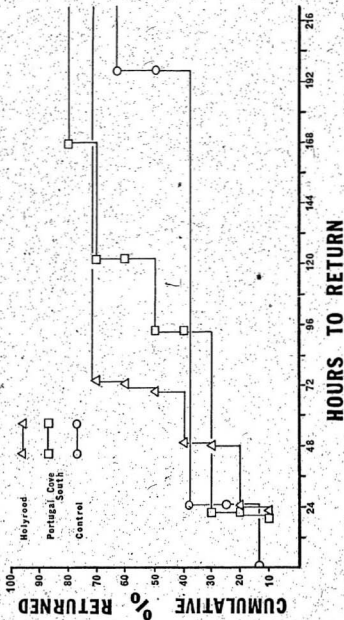


Figure 7. Cumulative percent returned and hours to return of Leach's Storm Petrels in Displacement 3, 1975, Holyrood - Portugal Cove South.

Table 2

Means, N's, and Standard Deviations for Return Times
in Displacement 3 and t-test Comparisons Between
Release Sites.

Portugal Cove South	n=8, \bar{X} = 83 hours, s = 55.96
Holyrood	n=7, \bar{X} =52 hours, s = 21.91
Controls	n=5, \bar{X} =89 hours, s = 99.08

Portugal Cove South vs Holyrood

One-tailed t-tests

- a) for independent samples: $t=-1.37$, $df=13$, $p>.10$ $p>.05$
 b) for correlated samples: $t=-1.67$, $df=6$, $p>.10$ $p>.05$
-

Portugal Cove South vs Controls

One-tailed t-tests

- a) for independent samples: $t=-0.14$, $df=11$, $p>.20$
 b) for correlated samples: $t=-1.45$, $df=4$, $p>.10$
-

Holyrood vs Controls

One-tailed t-tests

- a) for independent samples: $t=-0.97$, $df=10$, $p>.20$
 b) for correlated samples: $t=-1.22$, $df=4$, $p>.10$
-

Light birds gained weight between collection, $\bar{X} = 51.7$ g and return, $\bar{X} = 55.6$ g (correlated $t = -2.68$, $df = 9$, $p < .05$, two-tailed test). At return, light's and heavy's were no different in weight (see Figure 8). To explore this relationship further, return time was regressed on weight change. Positive weight change was associated with increased return times, $r = +.46$ ($F = 4.29$, $df = 1/16$, $p < .05$). The equation is Hours to Return = $81.46 + 4.41$ (Weight Change). It accounts for 21% of the variance in return time ($r^2 = .21$).

Discussion

The immediate question is whether or not the present evidence supports overland homing in Leach's Storm Petrel. The fastest Holyrood birds homed in 23 and 24.5 hours. In this time they either flew approximately 200 km or over 400 km. The furthest confirmed distance a Leach's Storm Petrel has flown in a 24 hour period is 350 km (Billings, 1968). In addition, Leach's Storm Petrels displaced distances comparable to 400 km took 3 or more days to return. These considerations suggest that the fastest petrels did not fly 400 km but instead took the shorter overland route.

The cruising flight speed of Leach's Storm Petrel has been estimated as slow as 24 km/h (Anne Linton, Pers.

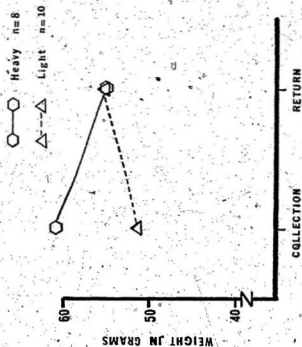


Figure 8. Weight at collection and return for heavy and light groups of Leach's Storm Petrels in Displacement 3, 1975.

Comm.) but may be considerably higher. Even at 24 km/h a petrel could fly 400 km in under 17 h. Billings' 350 km/day petrels averaged this speed for 14 days while they crossed the Atlantic. That they gained weight en route suggests they were not overly taxed. Finally, Holyrood birds flying the all water route had following winds down Conception Bay the night of their release. Next morning, the winds shifted to easterlies providing a favourable component for the homeward run to the island. These arguments suggest that even the fastest Holyrood homers may have flown the longest distance. At best then, this issue remains unresolved.

The weight data support and extend the conclusions of Displacement 2. Heavy birds definitely return sooner than light birds. Since heavy birds lose weight en route, while light birds gain weight, the hypothesis that recency of return from foraging explains weight differences is supported. However, if this were to comprise the entire explanation, light birds should be heavier at return than the heavy birds. There is some criss-crossing in weights between the two groups but the heaviest heavy's come back weighing more than the lightest of the light's. This suggests that sheer physical size also plays a role.

However the fact that only 21% of the variance in return time is accounted for by weight, indicates that other factors of equal or greater import to homing have yet to be

isolated.

Displacement 4, 1975

Previous releases indicate no marked effect on homing times by either distance or direction of displacement. To explore this further another orientation activity chamber test was planned at release sites of different direction and distance. These sites were Springdale on the north central coast of Newfoundland and Port aux Basques on the west coast of Newfoundland. However, complications in transportation arrangements resulted in Portugal Cove being substituted for Port aux Basques. Airline distances from Springdale and Portugal Cove to Middle Lawn Island are 290 km and 224 km respectively. The all water route from Springdale is about 730 km, 355 km further than from Portugal Cove (375 km to Middle Lawn Island; see Figure 1).

Following Displacement 3, it was hypothesized that

- a) heavy birds would return sooner than light birds,
- b) heavy birds would lose weight en route and c) light birds would gain weight en route.

Due to the lateness of the season, most of the eggs in the colony had hatched, meaning few adults were to be found during the day when searches for birds took place. Consequently no control group was gathered.

Method

Subjects

Twenty adult Leach's Storm Petrels were collected: 14 were incubating; 3 were found alone in burrows; 2 formed a pair; 1 was brooding a chick.

Apparatus

Carrying cases, stakes, compass, orientation activity chambers, and the triple beam balance, as previously described, were used.

Procedure

i Collection. On 17 August, 1975, between 12:00 and 16:00, petrels were collected. Procedures were the same as in previous displacements including division into heavy and light weight groups. Half of each group was assigned to each displacement site.

ii Displacement. All birds were transported to St. John's, Nfld. that night. On 18 August, the Springdale experimenters picked up their birds and drove to Springdale. Portugal Cove birds were handled for transfer like the Springdale birds and then replaced in the original vehicle to await release. At 23:00 a standard orientation activity chamber test was begun. One hour later at 24:00, birds were released from the chambers to N. S. E. W. in rotation. Between 20:00 and 22:00, one bird escaped in Portugal Cove.

iii Release Site and Weather Descriptions.

a) Springdale. The release site was in a field near the ocean at Springdale. Weather conditions were as follows: temperature, 14°C; wind, less than 8 km/h from 270°; visibility, unlimited; cloud cover, 80%; a 3/4 moon was visible at 180°; occasional sprinkles of rain fell late in the release.

b) Portugal Cove. The release took place in a clearing 100 metres in diameter in Portugal Cove about 1 km from the ocean. Weather was generally calm throughout: temperature, 15°C; wind, imperceptible; visibility, unlimited; cloud cover, 100%. There was a very bright sky due to the moon, light penetrating the cloud layer.

iv Burrow Checks. Checks for homers occurred four times daily, weather permitting (9 of a possible 56 chicks were omitted) from 19 August to 1 September, at the same times as checks for other displacements. From 3-7 September one check occurred nightly at 01:00. Homers were weighed and then returned to their burrows.

Results

Weather Conditions

The weather varied between 18 August and 25-26 August, the night of the last return. During 18-19 August, a low pressure system resulted in rain bearing 30 to 40 km/h winds from the SE. As the centre of the low passed, the winds

dropped to 25 km and shifted to SW bringing fair weather 19 August through the day of the 20th. The night of 20-21 August ushered through a high pressure ridge. This was associated with seven squalls bringing winds gusting to 50 km/h, rain, thunder, and lightning. Between squalls, winds remained about 25 km/h, skies were clear and the visibility unlimited. Winds dropped off 22 August as a low pressure system approached. During the night of 22-23 August, a deepening depression resulted in a gale with winds 40 to 65 km/h and much rain from the ESE. This system passed by the day of 24 August. Weather remained fairly calm (winds under 30 km/h) until 31 August. A storm with winds above 100 km/h struck from the ESE abating 2 September. Calm weather prevailed with occasional rain until 7 September.

Success and Return Time

Homing success and return time are depicted in Figure 9. Four birds (40%) returned from each site. Springdale birds averaged 122 h while Portugal Cove birds homed in \bar{X} = 137.5 h. These times were not significantly different (correlated $t = 2.33$, $df = 3$, $.10 > p > .05$, one-tailed test). Of the 8 homers, 6 had been incubating eggs, one was a single bird, and one was a member of a pair.

Weight and Return Time

Collection weights of the displaced birds were \bar{X} - light = 50.8 g, \bar{X} - heavy = 59.2 g. Success did not differ

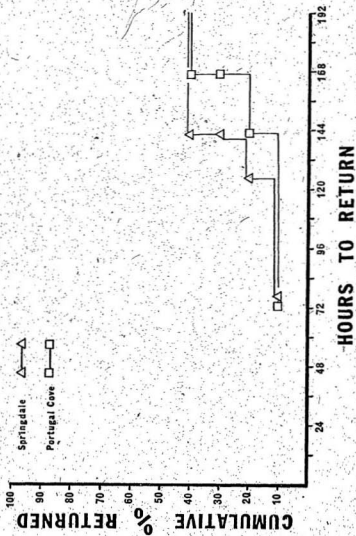


Figure 9. Cumulative percent returned and hours to return for Leach's Storm Petrels in Displacement 4, 1975, Springdale - Portugal Cove.

markedly between the groups, 3 heavys and 5 lights returned.

Heavy birds returned marginally sooner, $\bar{X} = 119.67$ h, than light birds, $\bar{X} = 135.80$ h, but not significantly so (independent $t = .58$, $df = 6$, NS). Heavy birds lost weight between collection $\bar{X} = 61.8$ g and recapture, $\bar{X} = 58.4$ g but again not significantly (correlated $t = .91$, $df = 2$, NS). Light birds significantly gained weight from 51.6 to $\bar{X} = 55.2$ g (correlated $t = 2.59$, $df = 4$, $p < .05$, one-tailed test).

Orientation Activity Chamber Tests

The raters agreed 89% of the time in their judgements of major activity direction and 100% of the time on activity level. No birds received scores less than (2). Thus all were included ($N=19$). One bird had escaped prior to the test.

The major activity directions and final headings are illustrated in Figure 10, A-D. On neither of these measures were the headings clustered significantly ($z < 1$, $n = 19$, $p > .10$, Rayleigh Test), nor were they significantly oriented homeward ($u < 1.1$, $n = 19$, $p > .10$, V Test). A Watson's and William's test comparing the two sites did not yield significance, major activity direction $F = 3.71$, $df = 1/17$, $.10 > p > .05$; final headings, $F = 0.0$, NS. Orientations relative to wind direction were computed. For Portugal Cove this was considered to be SE since that was the wind direction of the local weather system. However these were not significant

(See Figure 10, E and F.)

Discussion

The orientation activity chamber test, in conjunction with the previous one, suggests that Leach's Storm Petrel do not choose homeward bearings when in such test situations. Lack of downwind orientation may be due to the very low wind levels during the trial.

Performance, as reflected in both success and return time measures, was notably poorer in the present displacement compared to previous ones. Procedural differences possibly account for some of the decrement in performance. In the present displacement, the birds were held in captivity a minimum of 33h compared to a maximum of 12 in prior releases. Furthermore, the lateness of the season may have contributed to slower homing times and poorer success because the birds are more likely to be down on their fat reserves (Griffin, 1940; Matthews, 1954b). A greater amount of unfavourable weather probably augmented this. Whatever the cause, neither distance nor direction of displacement can be evoked as a reason. Holyrood is only a few km from Portugal Cove and yet birds from Portugal Cove took just as long to home as those travelling from Springdale. The extended homing times mitigate against any conclusions concerning possible overland homing by the Springdale birds.

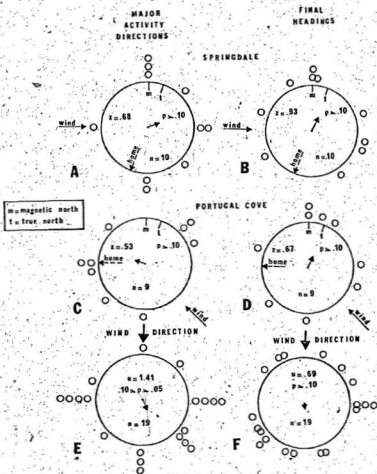


Figure 10. Major activity directions and final headings of Displacement 4 activity chamber tests - diagrams A-D. Diagrams E,F, present the same data plotted with reference to wind direction. Arrows in the centre of each circle depict direction and strength of the mean vector for that sample.

With only eight birds homing, it is not remarkable that weight differences were no more positive than they were. Even so, non significant differences were in the appropriate direction. To insure more birds home it may be advisable to increase the number of birds collected.

Displacement 5, 1976.

In Displacement 5, the effects of the following factors on homing performance were assessed: displacement inland; time in the burrow prior to displacement; collection weight and return weight; incubation shift length; sex; previous breeding experience; and previous displacement experience.

1) Displacement Inland. In the 1975 transisthmus releases, birds released from two different sites (near shore and far shore) homed-in similar times. This suggests the birds took similar routes and thus the far shore birds traversed the isthmus. However, the latency to return allowed sufficient time for even the fastest far shore birds to fly the longer all water route. Information lacking here concerns petrels performance when flying overland. For instance, if overland homing times are similar to over water homing times, assuming equal distances, then the hypothesis that the far shore birds traversed the isthmus is strengthened. To ensure overland flight, it was decided to displace a group of birds inland. For comparison two other groups were released simultaneously with the

inland group, one an equal distance away but at water's edge, the other on the home island.

2 & 3) Time in Burrow Prior to Displacement: Collection Weight and Return Weight. When sample size was large enough, the 1975 weight data were very clear. Heavy birds returned sooner losing weight en route while light birds homed later while gaining weight. Since incubating birds lose 2.2 g/day (Huntington in Billings, 1968), the above weight differences may largely be accounted for by short versus long incubation spells. To check this, the activity of the home burrow was monitored prior to displacement to determine when the last nest relief occurred. It was predicted that longer incubating birds would be lighter at collection, more likely to forage and return later weighing more at return than birds incubating a short time. Determining collection weights and return weights was necessary to test this hypothesis.

4) Incubation Shift Length. Gross (1935) observed that incubation shifts vary by 1 to 5 days and Wilbur (1969) noted that the average shift length was 3 days. However, some pairs seem to switch about almost nightly, while others are far less consistent averaging reliefs at the rate of 1 every 3 or 4 days (Wilbur, 1969). How this might influence homing is unknown. To explore this, incubation shifts were noted and their relationship with the other variables was checked.

5) Sex. Gross (1935) sexed by dissection seven birds caught in the act of digging and he discovered that all were males. Wilbur (1969) did not find any relationship between burrow re-use and sex but his study only covered one year. Furthermore, as he admits, the number of desertions caused by his activities may have masked any relationships. Other investigators (Davis, 1957; Richdale, 1963, 1965; Harris, 1969; Beck and Brown, 1971, 1972; Fisher, 1972) have found procellariiforme males frequent nest sites more often and have a greater site fidelity than females. That male Leach's Storm Petrels may be solely responsible for initiating burrow construction suggests that, similar to their related forms, they too have greater site fidelity. If so, then it may be expected that males either home sooner than females or that a greater percentage of males will return than females.

According to Serventy (1956) and Huntington (Pers. Comm.) the only way of sexing petrels in the field is at egg laying. At this time, a female Leach's Storm Petrel's vent is swollen, purplish and distended to 4 mm or more (Huntington, Pers. Comm.). Thus with all birds in which egg laying date was known, the condition of the vent was noted. Sex was assigned on this basis and on the basis of an association with the burrow of a bird of known sex.

6) Breeding Experience. Since breeding is usually delayed to the third or fourth season (Huntington and Burt,

1972), all breeders have ample opportunity to range widely and therefore probably all are experienced navigators. Even so it is likely that first attempt birds will be less efficient, have less fat reserves and thus more likely to abort their nesting attempt if they are displaced. There are three potential ways of identifying these individuals - date of egg laying, egg size and burrow depth.

i Egg laying date. In the Atlantic population, egg laying is asynchronous, extending over at least six weeks from the end of May to the middle of July (Palmer, 1962). The majority of the birds lay during a three week period between the middle of June and the end of the first week in July (Wilbur, 1969). Evidence from Hydrobates pelagicus (Davis, 1957) and Diomedea irrorata (Harris, 1973), indicates that the earliest layers are experienced breeders and later laying is an indication of inexperience.

Egg laying date may be significant in another way. The earlier a bird lays in the season, the more advanced will be its incubation stage by the time of displacement. Contrary to the norm, procellariiformes' urge to incubate seems to decline as the season progresses (Griffin, 1940; Marshall and Serventy, 1956; Matthews, 1954a, 1964); thus, early layers may be less inclined to home than later layers.

It may be that these two factors, inexperience, and stage of incubation, balance each other. In this case egg laying date

would not bear any direct relationship to homing performance. However, because both hypotheses are tentative, and both implicate egg laying date as important, it was decided to note the date of egg laying for displaced birds.

ii Egg Size. In four procellariiformes (Royal Albatross, Diomedea epomophora, Richdale, 1952; Short-tailed Shearwater, Puffinus tenuirostris, Serventy, 1967; Buller's Albatross, Diomedea bulleri, Richdale and Warham, 1973; and the Waved Albatross, Harris, 1973) it has been established that first laying females lay significantly longer narrower eggs, and that the width of the egg increases with successive layings. Harris used an egg index, $\text{Length} \times \text{Width}^2$ as his measure. This index was adopted for the present study.

iii Burrow Depth. Since males may be site specific, and clear out their burrows yearly, then the burrow may become deeper with each passing season. If so, then shorter burrows would be associated with first attempt birds. With this in mind, burrow depths were recorded.

7) Previous Displacement Experience. Matthews (1964) found that Manx Shearwaters displaced more than once over several seasons, improved their homing performance. He attributed this largely to habituation to the disturbance caused by the experimental procedure. To explore this in Leach's Storm Petrel, it was planned to locate as many birds as possible from the 1975 displacements and include up to 20 in the present release.

Method

Subjects

Fifty-nine adult Leach's Petrels were used. Of the 59, 42 had not been displaced before, were sexed, had their egg laying dates known, and burrows monitored. The other 17 had been displaced previously; eleven had previously returned as well. Sex and egg laying dates were not known for these birds. All birds were found incubating eggs except one. This one, a 1975 homer, was found as a member of a pair in a burrow without an egg.

Apparatus

Carrying cages and stakes were used as before. Weights were measured with a Pesola spring balance, 100 g scale. Vernier calipers were used for egg measurement.

A burrow monitoring system was developed to check for homers. This consisted of five 20 channel Esterline-Angus Event Recorders wired directly to switches placed in the burrow entrances. Most burrow switches activated their own separate pen. Because of the limitations imposed by the amount of wire needed to reach some distant groups of burrows, several burrow switches were hooked to one pen in four instances. Straw lattices were used in combination with switches in these cases so that it could be determined which of a group of burrows wired to the same pen had been entered.

Each switch consisted of an annealed nylon rod which was shoved into the peat to anchor the switch. Travelling up through

a bored out section in this rod was a stainless spring steel wire. This wire passed through a small stainless steel ring mounted in a screw-on annealed nylon cap. The switch was positioned so that the wire projected across the burrow entrance. To enter or exit the burrow a bird had to move the wire up or down. This caused the wire to touch the steel ring completing an electrical circuit. (For details see Appendix B.)

Procedure

1 Selection. A densely populated (2.6 burrows/m^2) area (150 m^2) of the colony was cordoned off.

Here, systematic daily lattice checks and explorations between 17 June and 6 July permitted the determination of the egg laying date in 64 burrows. When first found, the egg's length and width were recorded. Sex was known in 51/64 burrows. As soon as the egg laying date was established for a given burrow, its activity was monitored either with the event recorders or by lattice checks at 24:00, 02:00 and 14:00. This continued until displacement day.

Forty of the 64 burrows were selected for first consideration. These were chosen to represent as wide a range of egg laying dates as possible. The remaining burrows were designated as alternates, to be used in the event that no bird was found displacement day in one of the first choice burrows.

From 6-11 July, burrows of previously displaced birds were explored. Primary choices were those in which a bird displaced in 1975 was found incubating an egg in 1976. First

alternates were burrows in which a known mate to a previously displaced bird was found incubating an egg in 1976. All other displacement burrows in which definite signs of breeding activity were found formed the group of second alternates. Activity was monitored by daily lattice checks at all burrows from 27 June until displacement day.

ii Collection. All birds were collected 16 July. Before entering a burrow the condition of the lattice was noted. Since only 17 previously displaced birds could be located, 42 (a number divisible by 3) initial displacement birds were collected. Unbanded birds were banded. All were weighed and placed in carrying cases with some peat from their burrow.

Random assignments to one of three release sites of first the experienced birds and then the initial displacement birds assured an equal proportion of each type to each site. All burrows had switches placed in their entrances. The switches were wired to the event recorders. Lattices were placed over entrances in which more than one switch activated an event recorder pen.

iii Displacement. By 13:00, 40 birds had been transported to Lord's Cove. Twenty were driven to Portugal Cove South, 20 to a point 56 km south of the Bay d'Espoir Highway - Trans Canada Highway junction, on the Bay d'Espoir Highway (see Figure 1). Nineteen remained on the island but were carried down to the shore then back to an area just N of the hill on

the plain. At 22:30 releases began in all three places. Birds were singly tossed to N E S W in rotation.

For the two displacement groups the time of release was noted for each bird. The island control group birds were released in 15 minutes but individual times were not noted. Thus the median release time, 22:37, was considered the release time for all birds in this group.

iv Release Site and Weather Descriptions.

a) Bay d'Espoir Highway. The topography was gently rolling. Spruce covered hills. The release site was high, on a flat bull-dozed area, 100 m from the road. It overlooked a river 1 km to the west. The weather was very calm: temperature, 15°C; wind, 0-4 km/h from the north; cloud cover, 100% and high, visibility, unlimited.

b) Portugal Cove South. The birds were released 10 m from water's edge on a beach near the town pier. The weather was calm: temperature, 14°C; wind, 5-10 km/h from 200°; cloud cover, not discernible through light coastal fog; visibility, .4 km.

c) Middle Lawn Island. The release site was on the N side of the island on the sloping grassy plain. The weather was as follows: temperature, 13°C; wind, 3-6 km/h from 270°; cloud cover 75% and high; visibility, unlimited. Twice daily weather observations were continued for 14 days here.

v Burrow Checks. One person constantly monitored the

event recorder each night. Whenever a pen flicked, an assistant went to the appropriate burrow and explored the burrow by hand. Non-displaced mates, when found, were returned to their burrows and monitoring continued. If a homer was found, time was noted, and the bird was weighed then returned to its burrow. Monitoring of that burrow was then discontinued.

During the night of the 16-17 July one event recorder was not working. The malfunction was discovered before the release, and the burrows associated with it latticed beforehand. These were checked hourly throughout that night. The system was fully operational from the night of 17-18 July on.

On 16 September, all displacement burrows were rechecked in order to determine breeding success.

Results

Weather Conditions

Between 16 July and 31 July the weather was uniformly calm. Occasional rain and overcast occurred but winds remained under 15 km/h except for a brief 12 hour period, the evening of 24 July. Winds gusted to 40 km/h from the SSW. By 05:20 on the 25th the wind had dropped to 0 km/h.

Treatment of the Data

All the independent variables are evaluated in light of their effect on each of the following dependent variables:

return/no return (Homing success in previous displacements),
return time, return weight, and breeding success.

Displacement Inland

Release site had no effect on return/no return. Sixteen of 20 (80%) Bay d'Espoir Highway birds, 17/19 (89%) control birds and 18/20 (90%) Portugal Cove South birds homed. This was tested by correlating release site with return/no return. Release site was scored as (1) control, (2) Portugal Cove South, or (3) Bay d'Espoir Highway and return/no return as (1) or (0) respectively. There was no significant relationship ($r = -.11$, $F = .74$, $df = 1/57$, NS).

Return time and release site is illustrated in Figure 11. Controls returned in $\bar{X} = 76.82$ h, Portugal Cove South in $\bar{X} = 83.5$ h and Bay d'Espoir Highway in $\bar{X} = 113.52$ h. As the value for release site increased, return time increased, $r = +.29$, $F = 4.812$, $df = 1/46$, $p < .05$, multiple regression analysis. T-tests for correlated samples indicated all of this effect was due to the difference between Bay d'Espoir Highway and the other two. Thus the controls and the Portugal Cove South group were not different ($t = -.80$, $df = 16$, NS) but both differ greatly from the Bay d'Espoir Highway birds, $t > 10.0$, $df = 15$, $p < .0001$ in each case.

Control birds returned weighing $\bar{X} = 50.47$ g compared to Portugal Cove South, $\bar{X} = 50.25$ g and Bay d'Espoir Highway $\bar{X} = 51.06$ g. There is no significant relationship here, $r = +.06$,

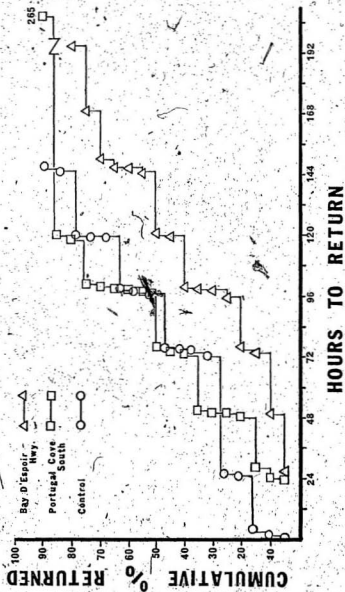


Figure 11. Cumulative percent returned and hours to return of Leach's Storm Petrels in Displacement 5, 1976. Bay d'Espoir Highway - Portugal Cove South.

$F = .22$, $df = 1/46$, NS, multiple regression analysis.

Of the control birds 11/19 (58%) raised a chick, while 9/20 (45%) of the Portugal Cove South birds and 6/20 (30%) of the Bay d'Espoir Highway birds raised chicks. This trend approached significance, $r = -.23$, $F = 3.14$, $df = 1/57$, $.10 > p > .05$, bivariate regression analysis. Of those that returned, 11/17 (65%) of the control 9/18 (50%) of the Portugal Cove South and 6/16 (38%) of the Bay d'Espoir Highway birds raised chicks. Again, the trend approached but did not attain significance, $r = -.22$, $F = 2.47$, $df = 1/49$, $.25 > p > .10$, bivariate regression analysis.

Time in Burrow Prior to Displacement and Collection Weight.

Neither time in burrow prior to displacement nor collection weight helped predict whether a bird would return or not ($r = +.06$ and $+0.07$ respectively, $N = 59$). Neither were related to breeding success, (nest time with breeding success, $r = +.10$ when $N = 59$ and collection weight with breeding success, $r = +.01$ when $N = 59$).

The relationships among time in burrow, collection weight, return weight, and return time are depicted in Figure 12. The longer a bird is on the nest, the less it will weigh at collection, $r = -.33$. The less a bird weighs at collection, the longer it takes to return, $r = -.35$. Birds lighter at collection tend to return weighing less than birds that were heavier at collection, $r = +.27$.

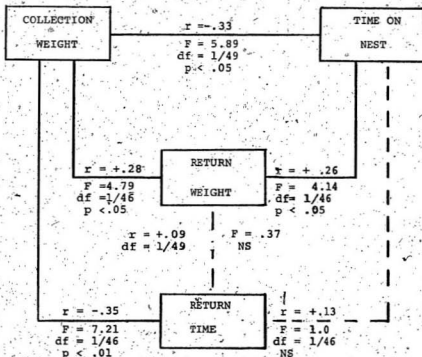


Figure 12. Strength of relationships among collection weight, time on nest, return time, and return weight in Displacement 5, 1976.

To find out if increased return time was associated with weight increases, weight change (the difference between a bird's collection weight and its return weight) was correlated with return time. This analysis approached significance, $r = +.23$, $F = 2.8$, $df = 1/49$, $.10 > p > .05$. When one extreme case was excluded (this bird returned 6 days after all the other birds in its group, all of which returned within 6 days of release), then $r^2 = .16$, $r = +.40$, $F = 9.4$, $df = 1/48$, $p < .01$ bivariate regression analysis.

Dividing the birds into heavy and light groups (50 g and over and under 50 g) and plotting the means, (see Figure 13), shows that heavy birds lose weight between collection and return (\bar{X} collection weight = 53 g, \bar{X} return weight = 51 g, $t = 1.75$, $df = 26$, $p < .05$, one-tailed test) and that light birds gain weight between collection and return (\bar{X} collection weight = 46 g, \bar{X} return weight = 50 g, $t = 3.52$, $df = 23$, $p < .005$, one-tailed test.)

As time on nest is increased, return weight increased, $r = +.26$. However the relationship between time on nest and return time, though in the predicted direction, was weak, ($r = +.13$, NS).

Incubation Shift Length.

The mean shift length per pair was determined by dividing the number of days between egg laying date and the displacement day by the number of disturbances of grass lattices, or by the

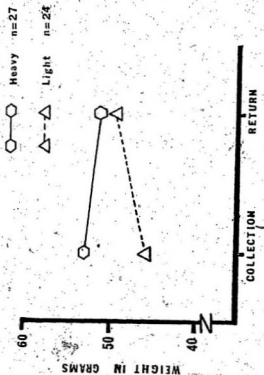


Figure 13. Weight at collection and return for heavy and light groups of Leach's Storm Petrels in Displacement 5, 1976.

number of burrow switch disturbances as registered by the event recorders. The mean shift length ($n = 42$) was 2.01 days, ($s = .54$).

Shift length bore no significant relationship with any of the dependent measures: shift length with return/no return, $r = -.22$, $F = 2.07$, $df = 1/40$, NS; shift length with return time, $r = +.21$, $F = 1.55$, $df = 1/34$, NS; shift length with return weight, $r = .26$, $F = 2.46$, $df = 1/34$, $.25 > p > .10$; shift length with breeding success when $n = 42$ (includes "no return" birds' burrows), $r = +.13$, $F < 1$, $df = 1/40$, NS and when $n = 36$ (only returned bird's burrows), $r = +.23$, $F = 1.91$, $df = 1/34$, NS (all are bivariate regression analyses).

Sex

Of the 42 sexed birds that were displaced, 25 (60%) were male and 17 (40%) were female. For correlations, males were scored (0) and females as (1).

Sex was not related to return/no return as 21/36 (58%) of the returning birds were male and 15/36 (42%) were female, $r = +.06$, $F < 1$, NS.

Male birds did not return earlier than female birds (\bar{X} male = 93.57 h, \bar{X} female = 88.88 h, $r = -.04$). Males returned weighing $\bar{X} = 50.24$ g, about the same as females, $\bar{X} = 52.23$ g, $r = +.24$, $F = 2.04$, $df = 1/34$, NS, bivariate regression analysis.

Of the 42 sexed birds, 12/25 (48%) males were associated with successful nesting attempts while 4/17 (24%) females were

associated with successful attempts ($r = -.25$, $F = 2.61$, $df = 1/40$, $.25 > p > .10$). Considering only those birds that returned, 12/25 (58%) males bred successfully and only 4/15 (27%) females bred successfully. This trend approached but did not attain significance, $r = -.30$, $F = 3.42$, $df = 1/34$, $.10 > p > .05$, bivariate regression analysis. In all burrows where a displaced bird did not return, the nesting attempt failed.

Breeding Experience

Neither egg laying date, egg index or burrow depth correlated significantly with any of the dependent variables (see Table 3). Egg laying date and egg index were related. The earlier the egg date, the larger the index, $r = -.32$, $F = 4.42$, $df = 1/40$, $p < .05$, bivariate regression analysis.

A breeding experience score was assigned to each burrow from which a bird was displaced. Judgments were based on comparisons of egg index, egg laying date and burrow depth to population norms established during the season, and on the banding history of the birds in question. Values allotted were as follows: (1) neither bird was experienced; (2) the displaced bird was inexperienced while the mate was experienced; (3) the displaced bird was experienced while the mate was inexperienced; (4) both were experienced. Frequencies of values follow: $n(1) = 4$, $n(2) = 3$, $n(3) = 2$, $n(4) = 50$.

Table 3

Relationships Among Breeding Experience Indicators and the
Dependent Variables in Displacement 5, 1976.

	Egg Laying Date	Egg Index	Burrow Depth
Return/ No Return	$r = -.0005$ N = 42	$r = -.18$ N = 42	$r = -.10$ N = 42
Return Time	$r = +.07$ N = 36	$r = -.10$ N = 36	$r = -.19$ N = 36
Return Weight	$r = +.06$ N = 36	$r = +.19$ N = 36	$r = -.07$ N = 36
Breeding Success	$r = +.01$ N = 42	$r = +.18$ N = 42	$r = -.11$ N = 42

Note: If $df = 1/40$, significance at the .05 level
is attained when $r = +.30$.

Breeding Experience was not related to any of the dependent variables: breeding experience with return/no return, $r = -.04$, $F = 1$, $df = 1/53$, NS; breeding experience with return time, $r = -.22$, $F = 2.83$, $df = 1/45$, $.10 > p > .05$; breeding experience with return weight, $r = +.21$, $F = 2.76$, $df = 1/45$, $.25 > p > .10$; breeding experience with breeding success, $r = +.15$, $F = 1.37$, $df = 1/53$, NS, all multiple regression analyses.

Previous Displacement Experience

A value of (0) was assigned for no experience and a value of (1) for having been displaced before. Treated in this manner, displacement experience was not related significantly to any of the dependent variables. Thirty-six of forty-two (86%) of the inexperienced birds returned while 15/17 (88%) of the experienced birds returned, $r = +.03$, NS. Inexperienced birds took $\bar{X} = 91.96$ h to return while experienced birds averaged $\bar{X} = 88.4$ h, $r = -.03$, NS. Inexperienced birds returned weighing $\bar{X} = 51.1$ g compared to $\bar{X} = 49.4$ g for experienced birds, $r = -.20$, $F = 2.34$, $df = 1/46$, $.25 > p > .10$, multiple regression analysis. Finally 16/42 (38%) of the inexperienced birds raised chicks while 10/17 (59%) of the experienced birds raised chicks, $r = +.19$, NS.

Since Matthews (1964) claimed handling experience is the important factor in experienced birds performing better, a new handling experience scale was constructed. Values were assigned

according to the following criteria: (0) no handling experience, (1) banded in a previous year (1974 or 1975), (2) banded in 1976 prior to displacement, (3) banded in a previous year and handled in 1976 prior to displacement, (4) previously displaced, (5) previously displaced and handled in 1976 prior to displacement, (6) previously displaced and tested in an activity chamber, (7) previously displaced, tested in an activity chamber, and handled in 1976 prior to displacement, (8) previously displaced, tested in an activity chamber and handled twice in 1976 prior to displacement.

The amount of prior handling experience did not predict whether a bird would return ($r = -.03$), nor did it affect time to return ($r = -.09$). There was a tendency for birds with more handling to have weighed less at return, $r = -.25$, $F = 3.13$, $df = 1/57$, $.10 > p > .05$, bivariate regression analysis. When only the returned birds' scores are employed ($n = 51$) then $r = +.30$, $F = 4.79$, $df = 1/49$, $p < .05$, bivariate regression analysis.

Of the 42 sexed birds, males had a significantly higher mean handling experience score ($\bar{X} = 1.32$, $n = 25$), than females ($\bar{X} = .65$, $n = 17$), $r = -.32$, $F = 4.44$, $df = 1/40$, $p < .05$, bivariate regression analysis.

To check the effect of being displaced on breeding success, the success in 36 burrows of returning birds from the cordoned off area was compared to the 1975 breeding success in 27 burrows from the same area. Burrows from which one adult was displaced

fledged 16/36 (44%) of their chicks, significantly less than burrows from which neither adult was displaced, 23/27 (85%), $t = 3.56$, $df = 61$, $p < .001$, one-tailed test.

Discussion

One of the successes in this displacement was the very high percentage of returns. A combination of good weather, optimal point in the breeding cycle, and relatively short time in captivity probably account for this². However, this high return rate may have created a ceiling effect such that none of the independent variables predicted whether or not a bird would return. Perhaps any effects there might have been are actually unimportant compared to the three factors mentioned above. If so future workers may wish to determine which or how much of these factors contributes to homing success.

The results of the inland displacement on return time are clear. A bird displaced inland takes longer to home than either one displaced an equal distance but released at water's edge, or one released on the home island. This suggests that petrels flying an overland route, as in the transisthmus releases, ought to be delayed. That none of the transisthmus birds were delayed indicates the selection of an all water route and thus provides no evidence of compass usage. Alternatively, the inland birds could have been delayed by having to determine their position to begin with - as opposed to either the control

²These variables intuitively seem powerful. However, with $N = 5$ displacements, a systematic evaluation was not warranted. For

birds or the Portugal Cove South birds who were released into familiar territory.

Interestingly, there was no difference between the controls and the Portugal Cove South groups, a finding paralleling that of Displacement 3. Once a petrel has been held in captivity for any length of time, its first priorities may be resting and foraging. In the present case, the home island birds may have had to make a two-way trip for foraging approximating the distances flown by the Portugal Cove South birds which may have foraged straight home. Furthermore, the Bay d'Espoir Highway group, by being displaced inland was actually deprived of the opportunity to rest or forage immediately after release. Because they sustained adverse conditions longer, they may have needed more time to recuperate than other groups and thus took longer to home. Also, the inland group was subjected to a higher risk of predation, though the specific effects in this case are unknown.

That return weight was not systematically related to release site suggests that in general petrels remain away until they have recovered from their experience in captivity. In addition, since they all arrive about the same weight, it may be argued that they return in much the same physical condition. This postulate is supported by the fact that breeding success was not significantly different among the three groups.

The weight-time relationships described in the present

a table presenting information pertaining to these variables
see Appendix B.

experiment corroborate and extend the conclusions of Displacements 2 and 3. The new information is that the length of time in the burrow is inversely related to collection weight and that length of time in the burrow is positively correlated with return weight. Both observations, in conjunction with previous findings suggest a competing motivational state hypothesis. As such, heavier birds would have a higher incubation drive. This wanes as time on nest increases and concurrently weight is lost. This latter is associated with a switch to a motivational state conducive to foraging. A foraging bird ought to gain weight. Thus a bird incubating a long time ought to (and does) return weighing more than when it was collected.

Overall size is again implicated as a determiner of return time. Heavier birds at collection returned sooner and weighing more than lighter birds. Contributing factors to larger sizes may be larger subcutaneous fat reserves, larger bone and concomittant musculature or a combination of both. At present this is unknown.

At first glance, there are two anomalies in the weight data. First, return weight is not related to return time. It might be expected that the lighter birds on the average would return later and weighing more than heavier birds. Thus return time and return weight would be positively correlated. However, expression of such a tendency appears to have been nullified in the present case by the size phenomenon just described.

Secondly, return time ought to be directly related to time on nest. That it was not suggests some of the birds freshest from foraging took long times to return. For instance, one petrel, captured after 7 h of incubating, took 4.25 days to return from Portugal Cove South losing 6 g enroute. By comparison, another bird, collected after incubating 7.5 h, homed from Portugal Cove South in 29 h gaining 4 g enroute. In addition to such inter subject variability, the accuracy of the time on nest measure is suspect. It ought to have been much more strongly related to collection weight because of the fact that organisms lose weight when they do not eat. Possible sources of error are: 1) different monitoring techniques - some burrows had lattices, some had switches; 2) incubating birds coming to the entrance and tripping the switch or disturbing the lattice; 3) other petrels prospecting for burrows tripping switches or disturbing lattices; 4) a high frequency of entrances and exits by two mates arriving with high incubation drives on the same night. In light of these factors, it is felt that more careful monitoring techniques would establish a direct return time - time on nest relationship even though this was not evident in the present data.

The sources of error just listed would also affect the accuracy of the incubation shift length measure. More disturbances than shift reliefs would result in deflated shift lengths. The validity of this argument rests on the observation that the

mean shift length has been observed by Wilbur (1969) to be 2.71 days and in previous years on Middle Lawn Island to be 2.68 days, both of which are greater than that recorded in the present experiment - 2.01 days. Another factor that may have decreased the effectiveness of this measure is that the shift length per pair may be less important than the mean shift length of the individual displaced bird. Because of these considerations, the question about shift length's effect on homing performance or breeding success remains open.

Sex does not seem related to homing performance though it may be to breeding success. It seems that displaced females are more prone to aborting their nesting attempt - an observation consistent with the idea that males have greater site fidelity. However, two relationships emerged in the data which may explain this effect. First handling experience increased the likelihood of breeding success for the returned sexed birds. Secondly, males were handled significantly more than females. Therefore the trend for females to abort more in the present study may be explained by the fact that they have received less prior handling than males.

The individual variables supporting the breeding experience scale deserve some comment. First, all three variables suffer from truncation of their ranges. The last egg laying date employed in the present study was 5 July while egg laying continued into late July. Assuming longer narrower eggs are

laid later in the season, the egg index range would also have suffered from this early termination of sampling. Burrow depths were limited by a) the person's reach exploring them (only marginally) and b) by the tortuous twists in some that prevented reaching the end. More importantly, increased variance may be expected in this measure because no relationship has been established between burrow architecture and age of the burrow.

Later egg laying was significantly correlated with longer narrower eggs. This result is consistent with the hypothesis that breeding experience is associated with earlier laying and the production of shorter wider eggs. Given a wider range of egg dates and indices, it would be expected that this relationship would prove stronger than reported here. Further support for this hypothesis would require determining the actual breeding experience and relating this directly to egg index and laying date.

The breeding experience scale itself suffered badly due to truncation. Whether or not this explains the weak effect on the dependent variables is an open question. However another possible contributor to the weakness of the relationships may be that all petrels of breeding age are experienced navigators.

Previous displacement experience in the present study had no significant effect on homing performance or breeding success. Matthews' (1964) previously displaced birds performed better on

second and third releases. However, his previously displaced birds had all returned. In the present study our previously displaced group included six birds which had not returned before; therefore our group was not as select as Matthews. Furthermore, factors which might have separated the experienced birds from the inexperienced birds (such as length of time in captivity, weather conditions and stage of breeding cycle) were all optimized in the present experiment.

The handling experience scale was a little more informative. It suggests that, providing a bird has not been displaced before, prior handling will produce habituation thus reducing the disturbing effect of displacement on breeding success. Even so, there is no indication prior handling experience had any effect on homing performance.

The insensitivity of the breeding success measure to the other biological (as opposed to displacement) variables may be explained by the overwhelming effect being displaced has on breeding success. Success rate was depressed from 85% to 44% by displacement. This finding represents the cost such research has in terms of the productivity of displaced birds.

Orientations, 1974-76.

Mature experienced birds of three species orient differently than immatures which are on their first migration or homing flight (European Starlings, Perdeck, 1967; Indigo Buntings, Emlen, 1972; and Homing Pigeons, Keeton, 1969, 1971a, 1972, 1974, Keeton and Gohert, 1970.) After Emlen, orientation chambers were used in order to determine if young Leach's Storm petrels oriented any differently than mature birds.

Method

Subjects

a) Adult Breeders. Birds found in nests incubating eggs were employed ($N = 87$). Of these 77 were run in 1974, and 10 in 1975.

b) Prebreeders. Birds found in July, purr calling from incomplete burrows were considered prebreeders. In total, 100 were run in July of 1976.

c) Chicks. Burrows in which downy chicks were located and banded were checked repeatedly in the fall until the chick was fully feathered. A total of 75 were located, 40 in September, October, 1975 and 35 during September, October, 1976.

Apparatus and Procedure.

The apparatus and procedure were the same as those detailed in Displacement 2 except the length of each trial was

60 min not 90 min. All trials were conducted on Middle Lawn Island. The number of birds run on any given trial varied from one to ten depending on the availability of subjects. The same cone scoring procedures were employed.

Results

Inter Rater Agreement

Only two raters were available for the adult bird cones. They agreed 78% of the time on major activity direction of each bird. Only one rater scored activity level.

The same three raters scored both prebreeder and chick cones. They agreed 87% of the time on the prebreeder major direction scores and 97% on the prebreeder activity level scores. The scoring of chick cones was more difficult and agreements on major activity direction occurred only 73% of the time. Activity level was agreed on 95% of the time.

Activity Levels

For 10-breeders no activity level scores were available so $n = 77$. Adult breeders ($\bar{X} = 3.71$) were more active than prebreeders ($\bar{X} = 3.17$, $t = 4.13$, $df = 175$, $p < .001$, two-tailed test). Prebreeders were more active than chicks ($\bar{X} = 2.24$, $t = 7.15$, $df = 173$, $p < .001$, two-tailed test). Adults were more active than chicks ($t = 8.90$, $df = 150$, $p < .001$, two-tailed test).

Exclusion of Subjects

Of the adult birds, 4 were excluded from further treatment because their activity level was one or below. Thus the number of final headings was 83. In addition, one bird did not display a preference in direction thus n for adult birds major activity directions equaled 82.

Of the prebreeders 2 were excluded due to inactivity leaving n = 98 major activity directions. Three birds got under the bottom of the cone and one other escaped prior to trial termination leaving n = 94 for final headings.

Sixteen chicks were not active enough to be included. For one more no major activity direction could be decided leaving n = 58 major activity directions. Final headings were not available for 2 birds beyond the sixteen leaving n = 57 for this measure.

Orientations

The major activity directions and final headings are displayed in Figure 14 for breeders, Figure 15 for prebreeders and Figure 16 for chicks. Breeders' major activity directions indicated a significant preference for the east (Mean angle = $99^{\circ} \pm 50^{\circ}$, 95% confidence interval; $r = .20$, $N = 82$, Ajne's $K = 272$, $p < .05$, Batschelet, 1972). The final headings were essentially random ($r = .07$, $N = 83$, Ajne's $K = 45.9$, $p > .10$). Prebreeders displayed a significant southwesterly heading on major activity direction scores (mean angle = $221^{\circ} \pm 50^{\circ}$, 95%

BREEDERS

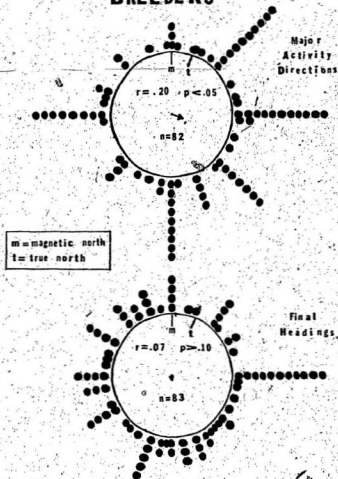


Figure 14. Major activity directions and final headings of the 1974-75 activity chamber tests with breeding Leach's Storm Petrels.

PREBREEDERS

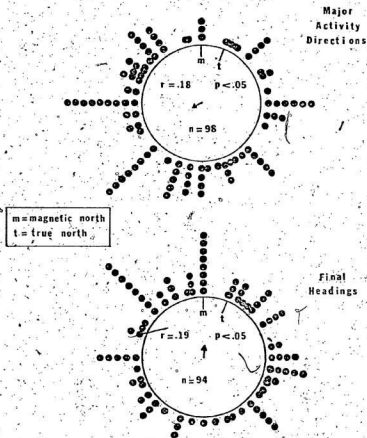
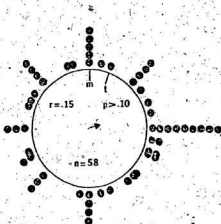


Figure 15. Major activity directions and final headings of the 1976 activity chamber tests with prebreeding Leach's Storm Petrels.

CHICKS

Major
Activity
Directions

m = magnetic north
t = true north

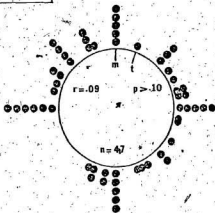
Final
Headings

Figure 16. Major activity directions and final headings of the 1975-76 activity chamber tests with Leach's Storm Petrel chicks.

confidence interval; $r = .18$, $N = 98$, Ajne's $A = 236$, $p < .05$) and a significant northerly orientation on final heading scores (mean angle = $345^\circ \pm 48^\circ$, 95% confidence interval; $r = .19$, $N = 94$, Ajne's $A = 250$, $p < .05$). Neither measure yielded significant orientation for the chicks; major activity direction, mean angle = 46° , 95% confidence interval $> \pm 90^\circ$, $r = .15$, $N = 58$, Ajne's $A = 116$, $p > .10$; final headings, mean angle = 46° , 95% confidence interval $> \pm 90^\circ$, $r = .09$, $N = 57$, Ajne's $A = 58$, $p > .10$.

Watson's and William's tests (Batschelet, 1972) were employed to test for differences among the three populations on both measures. Major activity direction scores were significantly different, $F = 16$, $df = 2/235$, $p < .01$ as were final headings, $F = 6.44$, $df = 2/231$, $p < .01$. In order to determine how much each pair of samples contributed to the overall effect, Watson's and William's test comparing two samples at a time were used (See Table 4).

Breeders were significantly different from prebreeders on both measures ($p < .01$). Breeders differed from chicks on final headings ($p < .05$) but not in major activity directions ($.25 > p > .10$). Prebreeders differed from chicks on major activity directions ($p < .01$), but not final headings ($p > .25$).

To check for downwind orientation, those birds which were tested during windy conditions had their scores replotted with reference to wind direction (see Figures 17, 18, 19). Significance

Table 4

Summary of Watson's and William's Tests (Batschelet, 1972)
 Comparing Different Subject Populations of Leach's Storm
 Petrel on Major Activity Direction and Final Headings.

Breeders vs Prebreeders

Major Activity Direction $F = 35.70, df = 1/178, p < .01$

Final Headings $F = 12.65, df = 1/175, p < .01$

Breeders vs Chicks

Major Activity Direction $F = 2.09, df = 1/138, .25 > p > .10$

Final Headings $F = 5.59, df = 1/138, p < .05$

Prebreeders vs Chicks

Major Activity Direction $F = 19.93, df = 1/154, p < .01$

Final Headings $F = 1.18, df = 1/149, p > .25$

BREEDERS

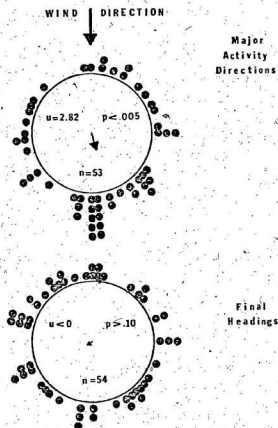


Figure 17. Major activity directions and final headings from breeder activity chamber tests that occurred in windy conditions. These data are plotted with reference to wind directions.

PREBREEDERS

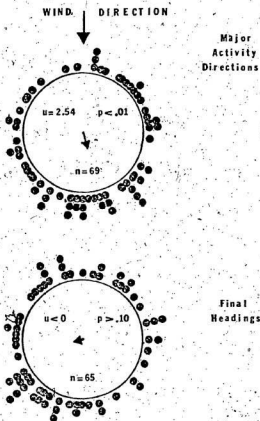


Figure 18. Major activity directions and final headings from prebreeder activity chamber tests that occurred in windy conditions. These data are plotted with reference to wind direction.

CHICKS

WIND DIRECTION

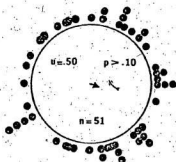
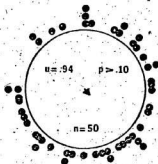
Major
Activity
DirectionsFinal
Headings

Figure 19. Major activity directions and final headings from chick activity chamber tests that occurred in windy conditions. These data are plotted with reference to wind direction.

was tested with the V test (Batschelet, 1972).

Breeders' major activity directions were significantly oriented downwind (mean angle = $165^{\circ} \pm 43^{\circ}$, 95% confidence interval, $u = 2.82$, $N = 53$, $p < .005$) while their final headings were not (mean angle = 286° , 95% confidence interval $> \pm 90^{\circ}$, $u < 0$, $N = 54$, $p > .10$). Prebreeders' major activity directions were also significantly oriented downwind (mean angle = $165^{\circ} \pm 48^{\circ}$, 95% confidence interval, $u = 2.54$, $N = 69$, $p < .01$) and their final headings were not (mean angle = 256° , 95% confidence interval $> \pm 90^{\circ}$, $u < 0$, $N = 65$, $p > .10$). Meanwhile chicks registered no orientation on either measure; major activity direction, mean angle = 107° , 95% confidence interval $> \pm 90^{\circ}$, $u = .5$, $N = 51$, $p > .10$; final headings mean angle = 139° , 95% confidence interval $> \pm 90^{\circ}$, $u = .94$, $N = 50$, $p > .10$.

Discussion

The clearest finding was the downwind orientation of both breeders' and prebreeders' major activity directions. This agrees with the results of Displacement 2.

That the final headings were not significantly oriented downwind may be an artifact of experimental procedure. At trial termination, the test chambers were approached from the downwind side, ostensibly to minimize disturbances possibly caused by olfactory cues emanating from an advancing experimenter. In the advent of less than stealthy approaches (frequent occurrences on

dark nights over boggy terrain clothed in squeaky rubber garments), the birds may have shifted to sections of the cone away from an oncoming E. Thus their final headings would be deflected upwind. At any rate, the failure of final headings to be oriented downwind is consistent with the findings of Displacement 2.

Interestingly, the chicks did not orient downwind on either measure. This suggests that for chicks, which have never flown before, wind direction is not a salient cue. Furthermore, that none of the analyses of chick data revealed significant orientation suggests that for chicks there is no one cue of highest priority.

The low activity level of the chicks was apparent both years in which they were run. This may reflect their difficulty in choosing a bearing. Consistent with this, breeders and prebreeders, both of whom displayed a general orientation, had much higher activity levels.

Knowing that the adults did orient leaves the task of determining the biological significance of the mean angles. If the final headings are dropped from consideration for reasons already discussed, it still remains that prebreeders oriented southwest, while breeders chose east south east, bearings that are separated by 122 degrees. Since on Middle Lawn Island either set of headings would carry a bird to open ocean, it is possible that both represent escape responses. However, even

if the motivations were similar, the stimuli the two groups were orienting by appear to have been different. Alternatively, both groups may have been orienting to similar cues, but these cues may have been emanating from different directions in the different years the groups were run.

By the same token, the differences registered between breeder and prebreeder activity levels may reflect differences due to different conditions prevailing in 1974 compared to 1976. Alternatively the discrepancy in activity levels may be a function of different sets of raters or of some real biological factor. Without more research, no decision can be made here.

There appears to be an anomaly concerning the mean angles of the three subpopulations. Thus, the mean angle computed from the chicks major activity directions is not significantly different from that of the breeders' but is significantly different from the prebreeders'. However, considering the extremely wide confidence intervals for the chick data (i.e. greater than $\pm 90^\circ$ at 95% level) it is difficult to assess the validity of this state of affairs. Again more information is needed.

The most profitable way to approach these data seems to be from the vantage point of which subpopulations are capable of orienting and which are not. In this light two things become clear. First breeders and prebreeders orient in a nonrandom fashion while chicks, by all measures do not. Secondly, breeders and prebreeders are sensitive to wind direction while chicks are

not. In this respect these data are consistent with those of Keeton (1969, 1971a, 1972, 1974) and Keeton and Gobert (1970) who showed generally that immatures demonstrated an increased scatter in flight bearings and needed several types of input in order to orient appropriately.

Food Sampling Study, 1975

Since the displacements were conducted during the breeding season, it was of interest to determine what sorts of marine cues might normally be used by Leach's Storm Petrels to orient during this time. Thus we attempted to determine foraging areas by collecting food samples during the summer of 1975. To catch birds we used a net.

Grubb (1971, 1974) contended petrels homing to their burrows relied mainly on olfactory cues. However, the vegetation on Kent Island (dense spruce forest) precluded the use of vision when birds were on the ground. Above the forest or over less densely forested habitat, vision may be important for guidance. Since Middle Lawn Island is treeless it was expected that the birds would use vision as much as the ambient light level permitted. In terms of our netting procedure, the number of collisions with the net should be inversely related to the amount of light available.

The sampling procedure also provided an opportunity to gain information about petrel's ability to remember landmarks,

specifically the position of the net. If the birds could remember the net's position, then the number of collisions with it ought to decrease over time.

Method

Subjects

All were adult Leach's Storm Petrels.

Apparatus

A "capelin" fish net (2.5 cm \times 2.5 cm mesh made of 2 mm diameter black twine) was used for netting purposes. The net stretched 10 m, was 3 m high and was supported at both ends and the middle. A small mechanical hand counter was used to count collisions with the net.

Procedure

On twenty occasions between 6 August and 10 October, the net was set up in one of four locations shortly after dark. Location 1 was on a plain at the base of the main hill. Netting occurred here eight times between 6 August and 27 August 1975. Location 2 was at the N end of the top of the hill and was used 29 August through 23 September 1975. Location 3 was on the S end of the top of the hill. Here netting occurred 24-25 September and 10 October 1975. Location 4, part way up the north-west slope of the main hill was used once 28 September, 1975. Netting continued 1-3 h depending on the success of collecting

food samples.

Each time any bird struck either the net or the supporting guy ropes, one collision was counted. These were tallied every 15 min and a new count begun. Most birds that fell to the ground or became stuck in the net were caught. Allowing the bird to flap its wings while maintaining a good grasp on it induced regurgitation of oil and solids. These were usually caught in a strategically held plastic bag. Once the bird had either regurgitated or been held for sufficiently long that the experimenter considered regurgitation unlikely, it was released. Food samples were transferred to bottles containing 10% formalin and shipped to Anne Linton at Dalhousie University for analysis. A few samples were obtained from birds caught on the ground during the course of other work.

Weather observations were made as a matter of course prior to sunset. The fraction of the moon illuminated and the proportion of time the moon shone during the netting session were derived from tables in the Astronomical Ephemeris for 1975.

Results

Food Sample Analysis

These data are provided courtesy of Anne Linton and form part of her Master's thesis on the Feeding Ecology of Leach's Storm Petrel (Dalhousie University).

In Table 5 the major food groups of the Middle Lawn Island birds are presented. Of all the species comprising these groups 81% by volume were vertical migrators only available at the surface at night. The other 19% were available at the surface during the night or day. Of all prey items, 50% were bioluminescent (Linton, 1978).

Most of the prey are generally available over the continental shelf surrounding Newfoundland. However, two myctophid fishes and the amphipod Hyperia galba (together amounting to 54% by volume of all food taken) are more promising indicators of foraging area.

Present evidence indicates that myctophid fishes are vertical migrators not found over shallow shelf areas. The closest water deep enough for myctophids occurs in the Laurentian Channel, coming within 125 km SW of Middle Lawn Island. Consistent with this, frequent records of Leach's Storm Petrel have been made in this area (Linton, 1978).

H. galba is an endo parasite of jelly fish of the genera Aurelia and Cyanea. The species Aurelia aurita and Cyanea capillata are both widely distributed along coasts in the NW Atlantic. The majority of both species are found within a few km of land with some Cyanea being found as far out as the 100 m contour line. Linton (1978) notes that most H. galba were virtually undigested.

Table 5

The Abundance (Number), Importance (Volume), Occurrence and Percent Occurrence of Individuals in Each Food Group in the Middle Lawn Island Food Samples, (N = 155), (Linton, 1978).

Food Group	Number	% Total Number	Volume (ml)	% Total Volume	Occurrence	Percent Occurrence
Squid	5	.17	15.00	3.36	4	2.58
Copepods	783	26.33	1.96	.44	57	36.77
Isopods	9	.30	.51	.11	8	5.16
Amphipods	1070	35.98	86.78	19.45	93	60.00
Euphausiids	849	28.55	31.62	7.09	33	21.29
Decapods	16	.54	13.61	3.05	18	11.61
Fish	242	8.14	296.70	66.5	127	81.94
Total	2974		446.18			

Note: Occurrence refers to the number of samples that a food type was found in.

Collision Data

The effect of wind speed, a factor thought to influence the number of birds visiting the colony, was considered separately. Visibility and percent cloud cover were included with the fraction of the disk of the moon illuminated and the proportion of the session the moon was out in the subjective assignment of a single illumination score for each netting session. Score values were either (1) very low level of illumination as under heavy overcast and fog, (2) moderate amount of light as under clear skies but very little moon, or (3) high amount of illumination as under clear skies and a full moon. The assignments were made three times by the same rater on 3 successive days. Average agreement among assignments was 86.7%.

A multiple regression analysis was run. Number of collisions per 15 min was the dependent variable. Included as independent variables were wind speed, session number/location, illumination score, and the three way interaction wind speed X session number X illumination score. The obtained r^2 was used to test the significance of the correlations of each of the independent variables as well as the two way interactions and the three way interaction with the dependent variable.

The number of collisions/15 min was negatively correlated (but not significantly so) with all three independent variables, (collisions with wind speed, $r = -.41$, $F = 3.85$, $df = 1/16$, $.10 > p > .05$; collisions with session number,

$r = -.33$, $F = 2.46$, $df = 1/16$, $.25 > p > .10$; collisions with illumination score, $r = -.32$, $F = 2.26$, $df = 1/16$, $.25 > p > .10$. The number of collisions/15 min was found to be significantly related to 2/3 two way interactions and the three way interaction, (collisions with wind speed X session number, $r = -.52$, $F = 6.01$, $df = 1/16$, $p < .05$; collisions with wind speed X illumination score, $r = -.46$, $F = 4.75$, $df = 1/16$, $p < .05$; collisions with session number X illumination score, $r = -.43$, $F = 4.14$, $df = 1/16$, $.10 > p > .05$; collisions with wind speed X session number X illumination score, $r = -.52$, $F = 6.17$, $df = 1/16$, $p < .05$).

Discussion

The food sampling data suggest that Middle Lawn Island petrels, during the later stages of the breeding cycle, forage from within a few km of the colony to probably not much further than the 125 km to the Laurentian Channel (Linton, 1978). Just as the two indicator species have been used by Linton to determine where the birds may be foraging, the birds may use the presence or absence of these prey as an indication of their location, especially at night or in dense fog.

The collision data is very suggestive. Because all but one of the interactions were significant, it may be argued that each of the independent variables had a real effect even though singly these effects were not powerful enough to be significant.

Full manifestation of the effects of wind may have been prevented by truncation of the wind speed range. Netting was not done under very windy conditions for fear of birds injuring themselves against the supporting poles.

For a variety of reasons, netting was not conducted on consecutive nights. Nor was the net up for an entire night. Thus the colony was exposed to the net after long, varying intervals, a procedure likely to reduce the rate of learning to avoid the net (Hoffman, 1966).

Expression of the effect of illumination level on collisions may have been limited by imprecision in the scoring system. Light meter readings in future would eliminate error here. Even so, the use of vision for net avoidance was substantiated by direct observation on bright moonlit nights. Under such circumstances, the net was clearly discernible at 50 m by the human eye. Birds could be watched approaching the net (either upwind or downwind) and then making abrupt course changes that carried them around or over.

Finally it is interesting to speculate on the relative importance of each of these variables. The wind speed seems to be the most important of the three - mainly as a determiner of the number of birds visiting the colony. That place learning has a greater influence on the number of collisions than illumination level may be advanced as a tentative hypothesis. It implies that in night flying petrels over presumably very familiar territory, knowledge of a place

proprioceptively is ascendant over visual information for guidance functions.

General Discussion

The present findings largely conform to current conceptions of homing. One important feature of some avian orientation systems is redundancy (Keeton, 1974, Emlen, 1975). That Leach's Storm Petrel also have redundancy in their systems is attested to by the fact their orienting behaviour is responsive to several kinds of cues. They may orient according to tactile cues (wind direction as in Orientations 1974-75 and Displacement 2), olfactory cues (Grubb 1971, 1974, Displacement 2) and visual information (Food Sampling Study).

A petrel could gain positional information by finding itself in the presence of either myctophid fishes or Hyperia galba, both being site specific prey items. As well, other features of the marine environment may prove useful to orienting petrels. This suspicion is heightened by the longer homing times of the one group deprived of immediate access to marine cues (Bay d'Espoir Highway group, Displacement 5). That inland displacement, an hypothesized information reducing procedure, resulted in longer homing times, suggests there is a limit to the number of redundant orientation systems of petrels. This would be in accord with previous work (Keeton, 1974, Emlen, 1975).

Another feature of birds' navigational systems is the shifting in the relative importance of cues when conditions change (Emlen, 1975). For Leach's Storm Petrel, wind direction seems to be the prime cue when in activity chambers while olfaction takes precedence for these same birds when free flying (Displacement 2). Some present evidence tentatively points to a greater reliance on memorized positions of obstacles for guidance about the colony than on visual information (Food Sampling Study).

That chicks randomly oriented in activity chambers (Orientations 1974-76), suggests they attach no particular importance to any one cue. This is in sharp distinction to both prebreeders and breeders which both oriented downwind when wind was noticeable. This age group difference is consistent with previous results (Keeton, 1974; Emlen, 1975) and implies that some learning essential to the orientational process occurs between the time a chick fledges and its subsequent return to the colony for breeding purposes.

It is unfortunate that the homing time results prevent conclusions about petrels' possible compass usage. At best, these data remain suggestive while providing further testimony to a sophisticated homing ability (Displacements 1, 3, 4, & 5). Demonstration of compass usage by the transisthmus release procedure requires far shore petrels to home directly or else for experimenters to determine the routes selected by homing petrels.

The former may require daytime release to ensure enough time for a bird to return to the colony the following night. This tactic has been avoided so far because of a concomitant increase in predation risk. Regarding the latter, one avenue remaining after the elimination of disappearing bearings (Griffin and Goldsmith, 1955; Billings, 1968), and activity chambers (Displacements 2,4) is radio tracking. Losses of experimental birds could be high as pilot work of Grubb's (1971) strongly suggest petrels can not or will not home to their burrow while carrying a 4 g transmitter plus antenna.

Another approach to the question of compass usage may be to investigate directly systems found relevant in other species. Of particular importance ought to be elucidation of the sun's role. Manx Shearwaters display a homeward orientation under sun that disintegrates under heavy overcast (Matthews, 1954a), suggesting the sun may be used as a compass. However, the appropriate clock shifting experiments which would demonstrate this (Schmidt-Koenig, 1965; Keeton, 1974) have yet to be performed. Similar investigations may yield comparable results for Leach's Storm Petrel.

In general, the monitoring of several biological variables indicated that only weight is a good predictor of homing performance (Displacement 2,3 & 5). More important determiners appeared to be time during the breeding cycle, intervening weather conditions and time in captivity, though these were not

systematically evaluated. Some prior handling raises a petrel's tolerance to the disturbance of displacement (Displacement 5).

Even with the nonbiological factors optimized, there was a great deal of variation in homing time unaccounted for by weight (Displacement 5). This suggests either emotionality or differing navigational abilities may be involved. Investigators in the future may wish to control for these by carefully selecting only the best of experienced homers. Certainly, advances in knowledge of pigeon homing have been preceded by the conscientious grooming of and selection for good homers (Keeton, 1974; Walcott, 1974).

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APPENDIX A
Cone Scoring Procedures

Cones were first folded along the N-S, E-W, NE-SW, and NW-SE axes; that is, a crease appeared every 45 degrees. Three raters scored them independently. Each rater would look into the cone and determine a major activity direction and an activity level. Major activity direction was operationally defined as the position relative to north (expressed in degrees, 0 - 360), where ink and scratch marks occurred in the greatest density and to the greatest height. The rater did not know where north was when making these judgements or the scoring recorded by the other raters. When two or more raters could not decide on a major activity direction, that bird's score was not considered further.

Activity level was scored on a scale of 0 to 5 with 0-1 representing no marks or only very few and 5 representing a cone marked and scratched densely over a large portion of its surface. The main purpose of the activity score was to provide a criterion for excluding inactive birds. Thus any individuals receiving a score of 0 or 1 were not included in further analyses.

The major activity direction score or activity level score to be used in calculations was chosen according to the following criteria.

- a) If two or more raters agreed exactly, then the agreed upon score was used.
- b) If there were no exact agreements, then if two observers' scores were within 45 degrees of each other for major activity direction, or 1 assigned rank for activity level, then the value

exactly between the two observed scores was used. If one score was intermediate (though not necessarily exactly so) among the set of three and within the above defined limits of the other two scores, then it (the intermediate score) was selected.

c) If there were no exact agreements and no scores within the defined limits, then the author's score was used.

An estimate of inter rater agreement was calculated as follows. Each rater's scores were compared to each of the other two raters'. If the scores were within 45 degrees for major activity direction or 1 assigned rank for activity level, then an "agreement" was counted. Greater differences were counted as "disagreements". Then a percentage of agreement was calculated according to the following formula.

$$\% \text{ Agreement} = \frac{\# \text{ of Agreements}}{\text{Agreements} + \text{Disagreements}}$$

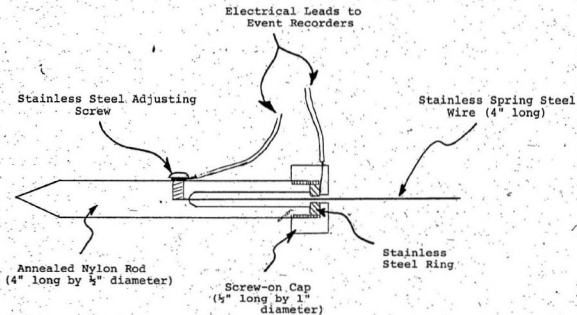
Thus for ten cones scored by three raters there were 30 comparisons (Agreements + Disagreements) of which only a certain percentage are agreements.

APPENDIX B

The Burrow Switch Used in the
Burrow Monitoring System,
Displacement 5

APPENDIX B

The Burrow Switch Used in the Burrow
Monitoring System, Displacement 5.



APPENDIX C

Date, Time In Captivity, Weather Conditions,
Composition of Subject Populations, Homing
Success, and Mean Hours to Return for All
Five Displacements

APPENDIX C

Date, Time In Captivity, Weather Conditions, Composition of Subject Populations, Homing Success, and Mean Hours to Return for All Five Displacements

Displacement Number	1	2	3	4	5
Date and Time of Release	C 23:30 h, 30 July, 1975	L 23:00 h, 9, August, 1975	H 00:20 h, 11 August, 1975	S 24:00 h, 18 August, 1975	B 22:30 h, 16 July, 1976
	A 00:30 h, 31 July, 1975	SL 23:00 h, 9, August, 1975	PS 03:00 h, 11 August, 1975	P 24:00 h, 18 August, 1975	PS 22:30 h, 16 July, 1976
	MLI 21:30 h, 31 July, 1975	MLI 23:00 h, 11, August, 1975	MLI 24:00 h, 12 August, 1975		MLI 22:30 h, 16 July, 1976
Time in Captivity	8 - 12 h MLI 3-4 h	All 4 1/2 - 7 h	All 9 - 12 h	All 32 - 36 h	All 12 - 17 h
Release Site Weather	C Clear Breeze from 180° 10% cloud	L Clear Breeze from 270° 10% cloud	H Clear Calm 20% cloud	S Clear Breeze from 270° 80% cloud	B Clear Light airs from 360° 100% cloud
	A Very foggy Breeze from 180° Sky not visible	SL Clear Breeze from 270° 40% cloud	PS Foggy Calm 100% cloud	P Clear No wind 100% cloud	PS Light fog Breezes from 200° Sky not visible

APPENDIX C (continued)

Displacement Number	1	2	3	4	5
Release Site Weather (cont'd)	MLI Calm Some fog patches 90% cloud	MLI Breeze from 125° Very foggy Sky not visible	MLI Light airs from 90° Very foggy Sky not visible		MLI Breeze from 270° Clear 75% cloud
Interim Weather	Good	Good	Fair	Poor	Good
Other Manipulations	None	Collection Weights Activity chambers test	Collection and return weights	Collection and return weights Activity chamber test	Collection and return weights
Composition of Displaced Population	25 Incubators 1 pair (2 birds)-with egg 1 pair-no egg (2 birds)	25 incubators 1 brooding chick 2 pair (2 birds) - no egg	26 incubators 1 pair (2 birds) - no egg 1 alone	14 incubators 1 brooding a chick 1 pair (2 birds) - no egg 3 alone	58 incubators 1 member of a pair
Composition of Hatching Population	No member of a pair returned	16 incubators 1 brooding a chick neither pair member	19 incubators 1 member of a pair	6 incubators 1 single bird 1 pair member	50 incubators 1 member of a pair

APPENDIX C (continued)

Displacement Number	1	2	3	4	5
Success	C 70%	L 60%	H 70%	S 40%	B 80%
	A 44%	SL 80%	PS 80%	P 40%	PS 90%
	MLI 80%	MLI 38%	MLI 63%		MLI 89%
\bar{X} Hours to Return	C 111.1 h	L 75.4 h	H 52 h	S 122 h	B 83.5 h
	A 70.2 h	SL 63.8 h	PS 83 h	P 137.5 h	PS 113.5 h
	MLI 99.4 h	MLI 26.9 h	MLI 89 h		MLI 76.8 h

A - Arnold's Cove
B - Bay d'Espoir Highway
C - Clarendville

H - Holyrood
L - Lories
MLI - Middle Lawn Island
P - Portugal Cove

PS - Portugal Cove South
S - Springdale
SL - St. Lawrence

